

MAMMALIAN FAUNA OF THE MIDDLE EOCENE KISHENEHN FORMATION,
MIDDLE FORK OF THE FLATHEAD RIVER, MONTANA

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ABSTRACT

The Kishenehn Formation is a unit of sedimentary rocks exposed largely in the cutbanks of the Flathead River and its tributaries in and around Glacier National Park in northwestern Montana and adjacent British Columbia. From these rocks along the Flathead's Middle Fork, which range from very fine-grained oil shales to and including pebble-cobble conglomerates, vertebrate and molluscan faunas of middle Eocene age have been collected over nearly 40 years by a combination of prospecting, with access by raft, to screen washing sediment from the most fossiliferous exposures. The mammalian fauna from the formation includes at least twenty-six taxa, ranging in size from tiny rodents and insectivores to a very large brontothere. A radiometric date of ca. 46.2 Ma was obtained from below the fossiliferous deposits. The age of the fauna, presumably within one or two million years younger than the radiometric date, is reinforced by the presence of the Uintan index taxon *Amynodon* Marsh, 1877, as well as the co-occurrence of an eomyid rodent referred to *Metanoiamys* Chiment and Korth, 1996, and the sciuravid rodent *Pauromys* Troxell, 1923. The fauna has a scarcity of Carnivora, which may reflect the real faunal composition. It is striking for its total absence of selenodont artiodactyls. Whether the latter should be attributed to geologic age, which is presumably early after these animals developed in North America or Asia, or is environmentally significant, must remain conjectural. Somewhat widely distributed in the North American west, earlier Uintan and/or Shoshonean mammalian faunas remain difficult to correlate, due at least in part to distinctive endemism or environmental uniqueness. The fauna also has indications of interchange between North American and Asian components at that time.

Of the twenty-six mammalian taxa recognized in the fauna, one is established as new, the rodent *Microparamys solis*, new species.

KEY WORDS: interchange with Asia, Kishenehn Formation, Middle Fork of the Flathead River, Uintan/Shoshonean

INTRODUCTION

The North American fossil record of Paleogene terrestrial vertebrates is skewed geographically, with a sparse record characteristic of the eastern parts of the continent, the few exceptions including coastal South Carolina (Schoch 1985) and the Gulf Coastal Plain (Beard and Dawson 2009). Paleogene vertebrate fossil localities occur through the more central and southern parts of the Rocky Mountain and Great Plains regions as well as through to southern California (Woodburne 2004). In addition to a distinctive Eocene fauna from the Canadian High Arctic (Dawson 1990; Eberle 2005), there are other later Cretaceous and Paleogene vertebrate localities north of the United States-Canadian boundary (Russell 1935; Fox 1990; Scott 2006; Eberle et al. 2014).

Russell's (1954) discovery of late Paleogene vertebrates from the Kishenehn Formation along the North Fork of the Flathead River in British Columbia added another northerly record, as did Storer's (1984) work in the Swift Current Creek deposits of southern Saskatchewan. To this record is here added a diverse Eocene mammalian fauna from northwestern Montana containing at least twenty-six taxa ranging from small multituberculates, insectivores, plesiadapiforms, primates, and rodents to the rhinoceros *Amynodon*

Marsh, 1877, and a very large titanothere. Unusual components of the fauna include a tarkadectine primate and the large titanothere. Although the faunal diversity is considerably less than the 53 mammal taxa of the Uintan fauna of Swift Current Creek, Saskatchewan (Storer 1984, 1996), it is closer numerically to the 22 taxa recognized in the early Uintan Whistler Squat locality of Texas (Campisano et al. 2014) and serves to document a geographically different sample, also interpreted as early Uintan.

Rocks of the Kishenehn Formation are exposed in three modern drainage basins in northwestern Montana and southern British Columbia, along the North, Middle, and South forks of the Flathead River and their tributaries. From cut banks along the former two of these rivers we collected both mollusk (Pierce and Constenius 2001, 2014) and vertebrate remains (Constenius et al. 1989). The Kishenehn Basin is the northernmost of a series of elongate, north to northwest trending late Paleogene to early Neogene structural and depositional basins. It is situated southwest of the Lewis thrust salient as a narrow, asymmetric graben 150 km long and 2 to 13 km wide (Figs. 1, 2). The Flathead normal fault system, the master structure that controlled basin origin, borders the Kishenehn Basin to the northeast and defines the eastern boundary of a belt of crustal stretching in the Cordilleran fold and thrust belt.

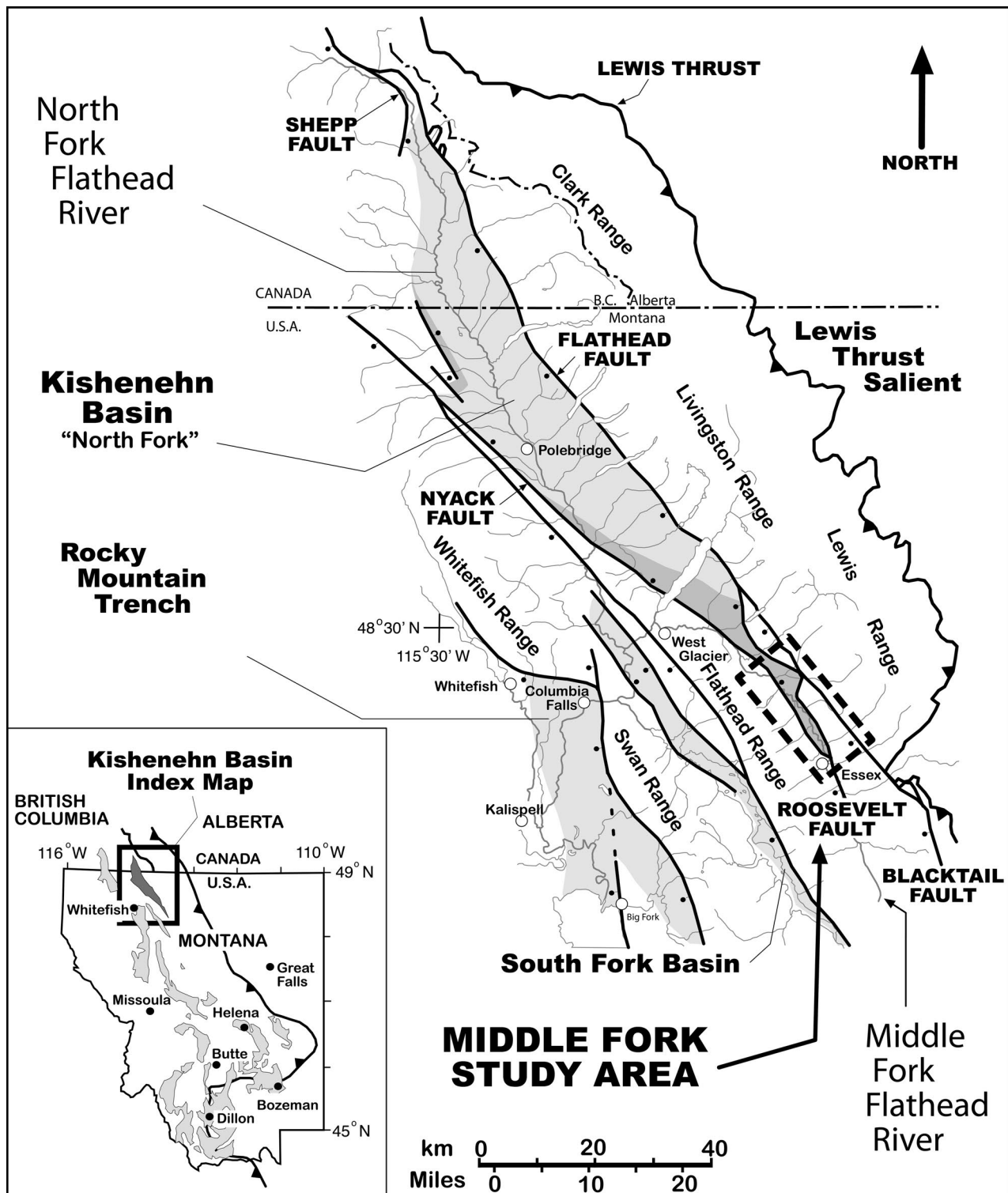


Fig. 1.—Kishenehn Basin shown with respect to adjoining grabens and half-grabens in northwest Montana and southeast British Columbia. Basinal areas with Tertiary strata exposed or subcropping beneath Quaternary deposits shown as middle Eocene (dark gray) and late Eocene to early Miocene (light gray). Note that the northwest-southeast geographic limits of the Kishenehn basin coincide with reentrants of salient of Lewis thrust fault. Inset lower left: index map of western Montana and southeast British Columbia showing location of Kishenehn Basin with respect to other late Paleogene extensional basins superposed on Cordilleran fold-thrust belt.

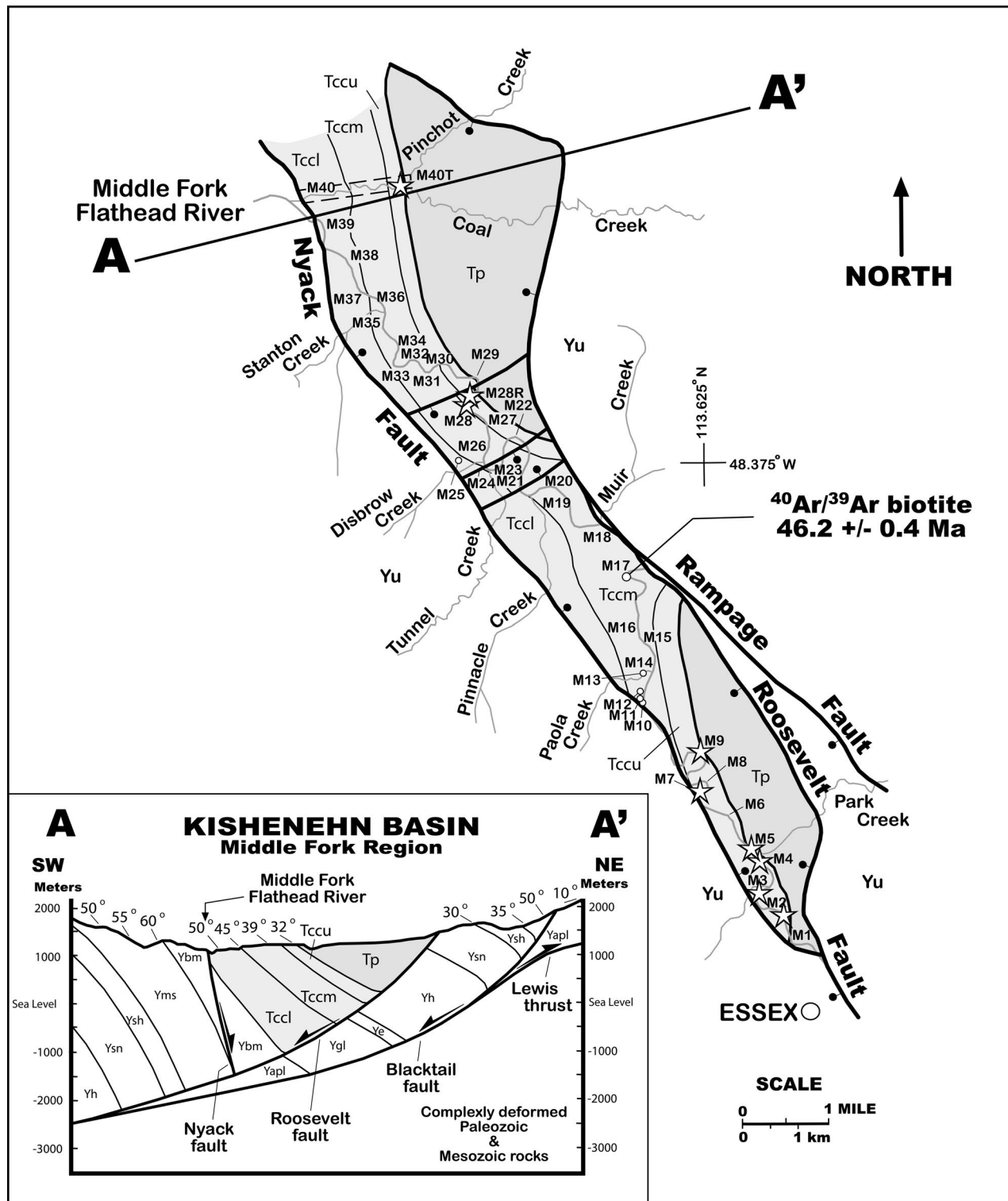


Fig. 2.—Kishenehn study area showing location of mollusk and vertebrate bearing localities (M) in the Coal Creek member along the Middle Fork, with geologic cross section of Kishenehn graben. Listric normal faults of Flathead fault system (Roosevelt and Blacktail faults) sole into extensionally reactivated part of Lewis thrust. Kishenehn strata display gradual flattening of dip up-section and thicken toward Roosevelt fault, a manifestation of concurrent sedimentation and slip on the curved fault surface. Rock unit abbreviations: Yapl, Ygl, Ye, Yh, Ysn, Ysh, Yms, Ybm, and Yu, formations of Proterozoic Belt Supergroup (see Constenius 1996); Tccl, Tccm, Tccu, Coal Creek Member (lower, middle, and upper sequences), and Tp, Pinchot member of Kishenehn Formation.

Normal faults bounding the Kishenehn Basin, South Fork Basin, and southern Rocky Mountain trench (Flathead Valley) are very large and have displacements of 15 km, 7 km, and 10 km, respectively (Constenius 1982, 1988, 1996; Van der Velden and Cook 1994).

The history of displacements of the Flathead fault system and related faults is recorded in sedimentary rocks of the middle Eocene to early Miocene Kishenehn Formation. Evidence for faulting concurrent with deposition of the formation is seen in sedimentary structures, facies relationships, provenance, paleocurrent directions, and most dramatically by the basin-wide stratal growth geometry of the beds (McMechan and Price 1980; McMechan 1981; Constenius 1982, 1996). The stratigraphic signature of synchronous normal faulting and basin fill sedimentation is seen in the formation as a systematic thickening of strata toward the basin-bounding listric normal fault, and a gradual flattening of dip in successively younger units (Dahlstrom 1970; McMechan and Price 1980). The strong rotational control on sedimentation associated with listric normal faulting results in a half graben or asymmetrical graben with a wedge-shaped sedimentary profile. Strata of the Coal Creek Member of the Kishenehn Formation dip 50° NE or more at the base and progressively decrease to 32° NE near the top of the unit, indicating that displacement and rotation along the Roosevelt and Blacktail fault segments of the Flathead fault system were synchronous with sedimentation.

The Kishenehn Formation in the Middle Fork region has been divided into a lower Coal Creek Member, which is composed predominantly of fine-grained clastic rocks, and an upper Pinchot Conglomerate Member, an assemblage of very poorly sorted, coarse-clastic rocks that conformably overlies the Coal Creek Member (Constenius 1981). Rocks assigned to the Coal Creek Member are a lithologically heterogeneous assemblage of sandstone, siltstone, coal, oil shale, marlstone and conglomerate that attain a thickness of 1150 m at the Coal Creek type section. Although the Coal Creek Member is lithologically diverse, its status as a member is justifiable on the basis of its overall light gray color and fine-grained character. Coal Creek strata are subdivided into three sequences (Figs. 3, 4), each bounded by gradational contact: a lower sequence, consisting primarily of profundal lacustrine and lacustrine-deltaic deposits; a middle sequence, consisting of alternating profundal lacustrine, lacustrine delta and fan-delta, and paludal strata; and an upper sequence composed of lake margin, paludal and fan-delta deposits (Carroll and Bohacs 1999). Strata of the lower sequence of the Coal Creek Member are light grey and light greenish grey, about 550 m thick and consist primarily of carbonaceous siltstone and very fine-grained to coarse-grained sandstone that display climbing ripple and horizontal stratification. Sub-bituminous coal, claystone and mudstone, oil shale, marlstone and conglomerate are also found, but to a much lesser extent, in the lower sequence. Oil shales have cumulative thicknesses up to 40 m in the lower sequence.

Lithologic, geochemical, and stratigraphic characteristics combined with facies associations and fish, aquatic mollusks, pollen, and insect fossils suggest that these strata are profundal lacustrine and lacustrine delta deposits (Curiale et al. 1988; Greenwalt and Constenius 2014). Fossil mollusks are very rarely found in sandstones and siltstones of this unit but the oil shale beds produced a number of aquatic examples, albeit with shells that are often partially or completely crushed.

The middle sequence of the Coal Creek Member is a distinctive light grey, well stratified unit that is exposed at numerous localities along the Middle Fork of the Flathead River. Lithologically, these rocks are heterogeneous, consisting primarily of oil shale, marlstone, sandstone, and siltstone with subordinate amounts of sapropelic coal, claystone and mudstone (Constenius and Dyni 1983; Bourke 2005). The thickness of the middle sequence is approximately 500 m, of which up to 45 m is oil shale. Detailed examination of the oil shale reveals that it contains rhythmite couplets (varves) comprised of three distinct layers: a lower thick gray layer of siliciclastic silt grains, a thin medial layer of calcite particles, and an upper black carbonaceous layer interpreted as a relict microbial mat. The respective provenance of these couplet materials within this rhythmite sequence are: angular-subangular silt sized grains of quartz and feldspar (potassium and sodium) thought to be eolian in origin, calcite precipitation related to lake warming and resultant whiting event, and a microbial mat layer comprised of several carbonaceous laminae (Greenwalt et al. 2015). The preservation of fossil insects within the microbial mats is extraordinary, with some containing traces of blood and colored pigment, and as a consequence the oil shales of the middle sequence are now recognized as a Konservat-Lagerstätte (Briggs 2013; Greenwalt and Constenius 2014). Insects and other arthropods (*Daphnia*, spiders, and ostracods) are also known from shales in the lower Kishenehn deposits. To date, 17 orders of insects have been identified (Greenwalt et al. 2015). The Kishenehn Formation insect fauna is dominated by Diptera and Hemiptera and is one of the best sites in the world for mosquito fossils with nearly 100 specimens collected to date. The insect fossils are unusually well preserved (Greenwalt et al. 2013, 2016). There is a strong taphonomic bias that favors preservation of very small (< 5 mm) insects; specimens larger than 1 cm in length are rarely preserved. In the last several years, over 40 new species of insects have been described.

Interstratification of oil shale and marlstone with sandstone, siltstone, mudstone, claystone, and sapropelic coal suggests that strata of the middle sequence were deposited in an anoxic alkaline and alkaline lacustrine regime (Demaision and Moore 1980; Curiale et al. 1988), replaced at times with deltaic and paludal conditions. Aquatic snail fossils abound in this unit and in places form a key 30–35 m thick stratigraphic marker known as the “Gastropod Zone,” which is typified by layers of white shells of the genus *Biomphalaria* surrounded by black sapropelic coal

KISHENEHN FORMATION Coal Creek Type Section

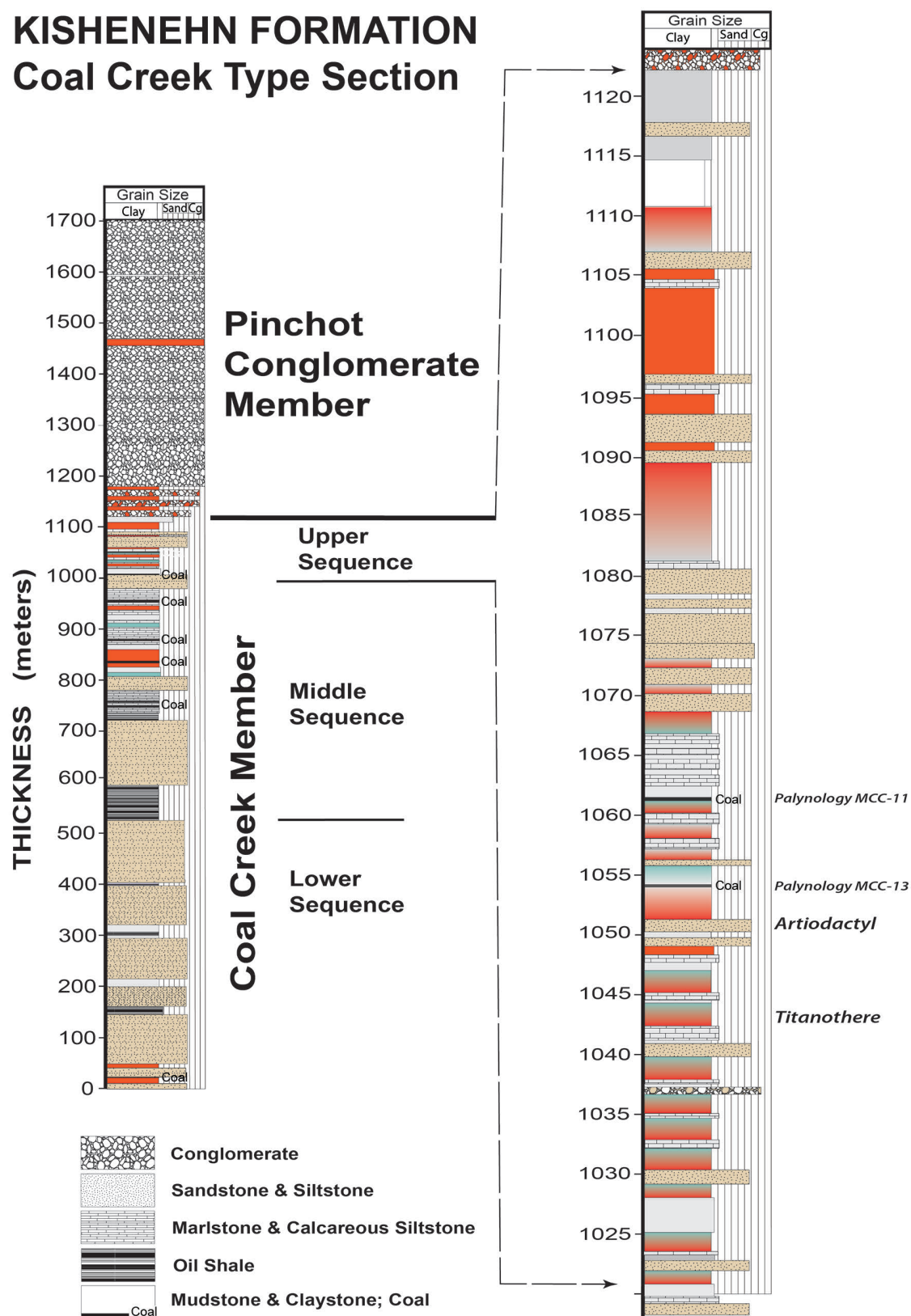


Fig. 3.—Kishenehn Formation, Coal Creek type section.

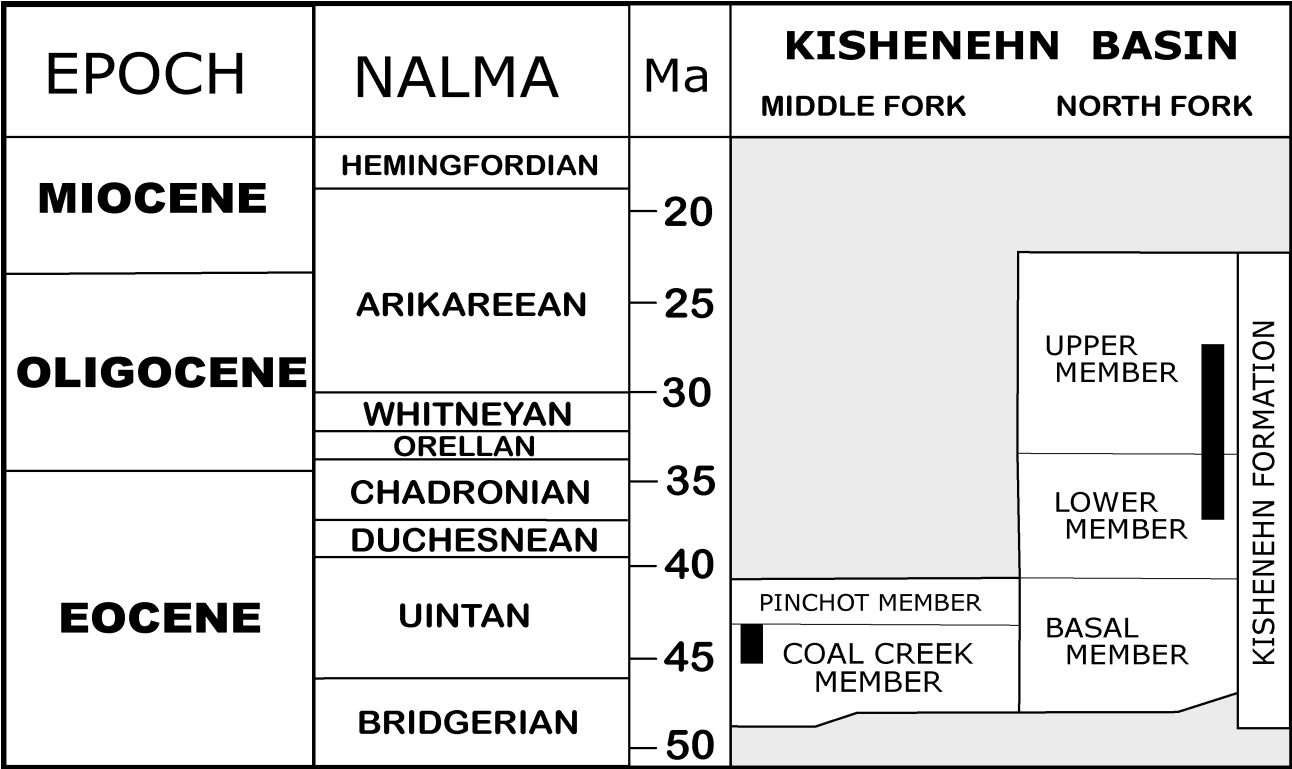


Fig. 4.—Stratigraphic chart showing correlation of Kishenehn Formation units in North Fork region to those in Middle Fork region relative to North American Land Mammal Ages (NALMA). Range of fossil-bearing units containing mammals in each region shown with black bars.

(Bourke 2005; Pierce and Constenius 2014) (Fig. 4). In terms of paleontological study, the shells of fossil gastropods and bivalves are prevalent but often crushed and distorted in these compacted and brittle shales.

Typically, the upper sequence of the Coal Creek Member consists of a mixed assemblage of marlstone, sandstone, siltstone, conglomerate, claystone, mudstone, and lignite. Strata of the upper sequence attain a thickness of about 100 m. Beds of variegated maroon to red-brown, red-brown and grey-green sandy mudstone and occasional conglomerate give outcrops of the upper sequence a distinctive pinkish cast in contrast to dominantly light grey color of the outcrops of the lower and middle Coal Creek sequences (Fig. 5). These variegated mudstones are thought to represent sediments deposited on the distal lobe of an alluvial fan and fan delta system where variations in water level resulted in intervals of subaqueous deposition alternating with subaerial exposure and development of paleosols. In spite of the deep red-brown coloration suggestive of paleosol development, the presence of aquatic fossil mollusks throughout much of this unit indicates that it is largely subaqueous. Lake margin, fan-delta, and paludal sedimentation is recorded in the marlstone, sandstone-siltstone-mudstone, and coal deposits, respectively. Mammal fossils are found almost solely in mudstones and sandstones of this unit, and it also produces the richest

variety and best preserved examples of terrestrial and aquatic gastropods (Pierce and Constenius 2014).

The Pinchot Conglomerate Member is a thick succession (200 to 700 m, estimated) of crudely stratified mudstone, sandstone, and conglomerate. Rocks of the Pinchot Conglomerate are identified by their maroon red-brown and red-brown color, extremely poor sorting, and coarse-clastic nature. Lithologically, these strata consist of: sandy mudstone and siltstone that grade to muddy sandstone, and are calcareous in part; matrix-rich sandstones are comprised of varicolored angular to subround, sand and pebble-sized lithic clasts of Proterozoic Belt Supergroup; and pebble-boulder conglomerates with abundant mudstone and/or sandstone matrix material. Lithic clasts in conglomerate units consist entirely of angular to subrounded Belt rock fragments that attain a size of up to 2.5 m. Beds of grey, sandy conglomerate with round to subround lithic clasts occur rarely. The extreme textural immaturity, reddish color, and coarse grained nature of the Pinchot Conglomerate Member suggest that these strata record episodes of rapid deposition of material by mechanisms such as debris flows and ephemeral braided streams punctuated by depositional hiatuses and paleosol development in the proximal and medial parts of an alluvial fan system. No fossil mollusks or vertebrates have been found in this unit.

The age of the Kishenehn Formation is important re-

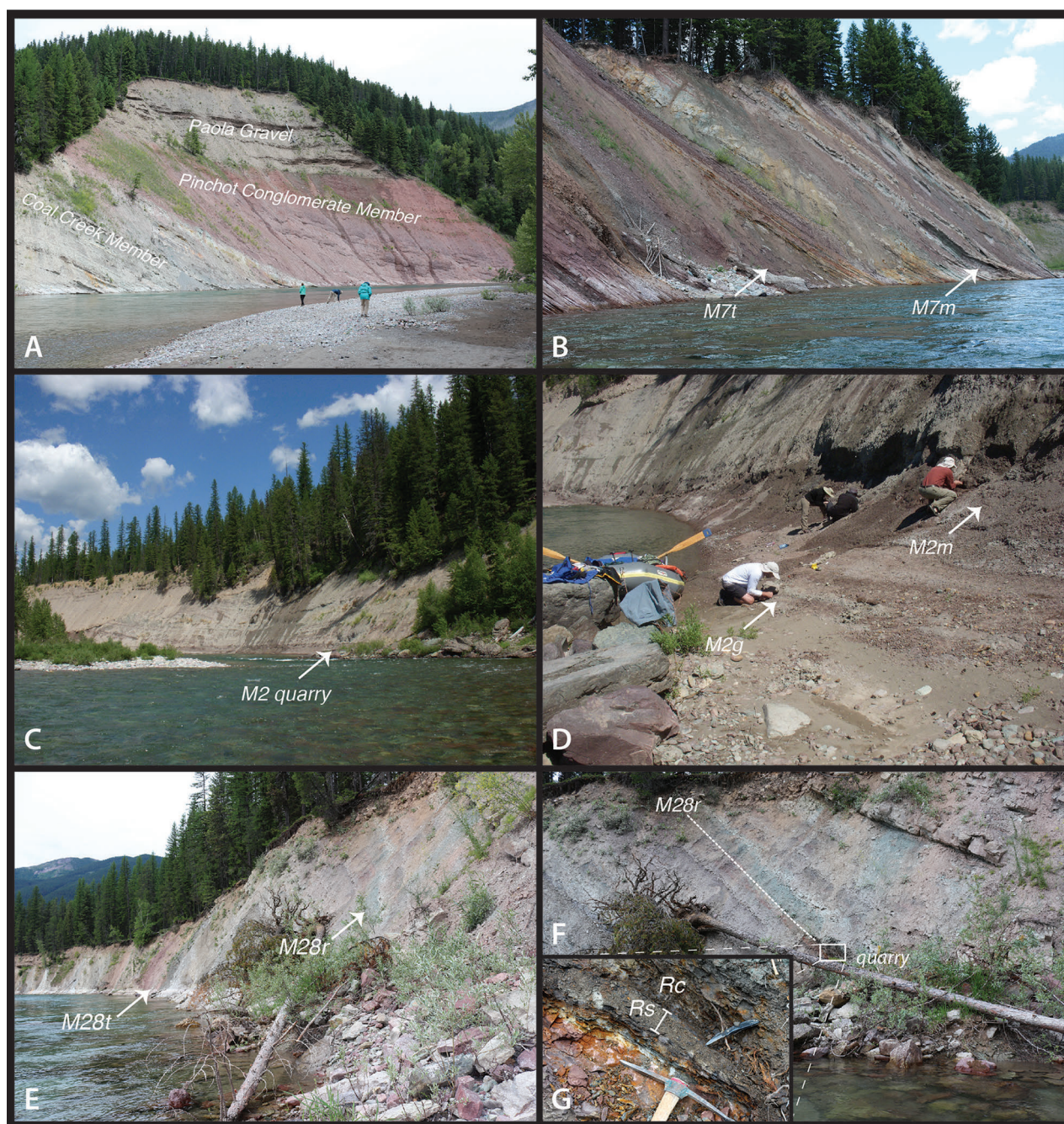


Fig. 5.— **A**, outcrop of the two members of the Kishenehn Formation, the Coal Creek and Pinchot Conglomerate members, overlain by the Paola Gravel. View looking northeast of cutbank locality M-28; **B**, locality M-7 showing upper sequence Coal Creek Member strata dipping northeast about 39 degrees. M-7 quarry sites: M7m, mammal site, and M7t, turtle site. View to north; **C**, M2 locality viewed from south; **D**, M2 quarry sites: M2m, fossil mammal bearing bed, and M2g, fossil gastropod bed. View to north; **E**, locality M-28 viewed to west. Strata of upper sequence Coal Creek Member dipping northeast at about 36 degrees. Locations of Tarkadectes and Rasmussen beds denoted by M28t and M28r, respectively; **F**, Rasmussen bed and quarry viewed from south; **G**, view of Rasmussen bed with knife and Marsh pick for scale. Bone producing layer, labeled Rs, is a 5–8 cm thick, gray, friable, coarse-grained sandstone-granular conglomerate overlying red brown mudstone. The upper part of the Rasmussen bed, Rc, is a coaly mudstone that contains abundant fossil leaf and seed impressions, amber, and mollusks.

TABLE 1

ID	Material	⁴⁰ Ar/ ³⁹ Ar	³⁷ Ar/ ³⁹ Ar	⁴⁰ Ar*/ ³⁹ Ar	Rad (%)	Age (Ma)	±1s (Ma)	⁴⁰ Ar	J
2606-1	Biotite	1.78	0.0096	1.44	80.9	45.196	0.872	3.0799	0.017588
2606-2	Biotite	1.96	0.0262	1.49	76.3	46.813	1.563	8.2298	0.017588
2606-3	Biotite	1.69	0.0549	1.46	86.9	45.880	0.429	6.8457	0.017588
2606-4	Biotite	1.97	0.0150	1.40	71.2	43.885	0.745	4.0551	0.017588
2606-5	Biotite	1.98	0.4692	1.42	71.7	44.433	0.580	5.866	0.017588
2606-6	Biotite	1.76	0.0085	1.46	83.1	45.857	0.548	4.8439	0.017588
2606-7	Biotite	1.69	0.0216	1.55	91.7	48.600	0.643	8.5876	0.017588
2606-8	Biotite	1.74	0.0124	1.45	83.2	45.411	0.647	9.28	0.017588
2606-9	Biotite	1.82	0.0088	1.44	78.9	45.049	0.634	9.4306	0.017588
2606-10	Biotite	1.67	0.0131	1.53	91.6	47.984	0.582	6.9068	0.017588
2602B-2	Biotite	1.59	0.1724	1.51	94.9	47.225	0.385	6.8713	0.017588
2602B-5	Biotite	1.65	0.2057	1.42	85.7	44.437	1.438	5.0675	0.017588
			0.0848				46.169	0.405	n=12

Robert C. Walter, Institute of Human Origins, Berkeley, CA, February 15, 1990
The Pinnacle Ash biotites yield quality data; with low ³⁷/³⁹ ratios, high %⁴⁰Ar* values and low analytical uncertainties. The grain-to-grain variation in age is greater than expected, which may indicate either contamination or alteration imposing a systematic error on the data. However, these discrepancies are relatively minor, and the mean age of 46.2 +/- 0.4 Ma, as shown in the bottom row of mean values, is a reasonable first order assessment.

gionally as it defines the time of initial crustal extension in the region and, consequently, as an upper time limit of contractile deformation (Constenius 1996; Constenius et al. 2003). Age-dating of a tephra from the middle sequence of the Coal Creek Member established a middle Eocene age for this unit (⁴⁰Ar/³⁹Ar biotite age of 46.2 ±0.4 Ma; zircon fission-track age of 43.5 ±4.9 Ma) (Constenius 1996; Table 1). The mammal bearing deposits of the upper sequence of the Coal Creek Member are about 300–350 m upsection from the dated tuff and we estimate their age to be about 44–45 Ma, close to the well-constrained radiometric age of 44.88±0.04 Ma for the early Uintan of Texas (Campaisano et al. 2014).

Fossil leaves and other megafloral remains have been found in the Middle Fork Kishenehn sediments, particularly in sandstone, oil shale, and coal deposits. The Kishenehn megaflora is moderately diverse but dominated by the platanoid *Macginitea augustiloba*, which indicates a humid, subtropical paleoclimate. Preliminary identifications show that other plants in the flora include *Cercidiphyllum*, *Metasequoia occidentalis*, Fagaceae, *Betula* or *Alnus*, *Castaneopsis* or *Castanea*, *Populus* sp., *Salix* sp., and *Malus* sp. Ranges of the known forms suggest a late Eocene date, but this is not consistent with known radiometric dates (Hickey, written communication, 1988).

The ~1000 m thickness of stacked lacustrine strata in the Coal Creek Member of the Kishenehn Formation in the Middle Fork region suggests a large, persistent perennial lake system. The presence of alluvial fans and fault proximal coarse-clastic detritus derived from the footwall

of the Flathead fault system (locally the Roosevelt fault, Fig. 2) combined with faunal, floral and oxygen isotope evidence (Constenius et al. 1989; Fan et al. 2016) suggest that densely wooded mountains paralleled the basin to the northeast and rose at least 2000 m and perhaps as much as 4300 m above the basin, much as they do today.

Further interpretation of the paleoenvironment based on previously studied fossil mollusks shows that they are divisible into three groups. Group I is a relict tropical wet fauna, existing in basinal waterways whose modern analogs live in the Caribbean and Central and South America. Group II is a subtropical, semi-arid fauna with modern analogues ranging from the north coast of the Gulf of Mexico, across the southern United States and northern Mexico to southern California and the Baja peninsula. Group III is a humid, warm temperate fauna that was transported from mountains east of the basin and deposited in fan-delta and lake margin settings. Modern analogues of these taxa are common in the east-central United States. The unusual co-occurrence of these climatically disparate groups of fossil mollusks is a manifestation of the large paleo-topographic relief, perhaps greater than 2000 m, that existed between the valley floor and the mountains (Pierce and Constenius 2014). The fossil mammal record, composed mostly of friable teeth that would not be preserved intact following extended transport, is composed of taxa that were not moved far and so members of the mammalian fauna may be presumed to have been inhabitants of a humid warm temperate area suggested by the warmest climate mollusks. Similarly warm climatic conditions have

been postulated also for several more westerly non-marine formations of Washington and British Columbia (Mustoe and Gannaway 1995).

MATERIALS AND METHODS

The non-marine sedimentary rocks of the Kishenehn Formation were first reported by G.M. Dawson (1886:52B) from southern British Columbia. Our attention was called to the vertebrate fauna of the formation by Russell's investigation (1954) of its deposits, from which he described fossil mammals considered to be Duchesnean and/or Chadronian NALMA, both now regarded as late Eocene (Fig. 4), an interval that we were investigating elsewhere (Black and Dawson 1966). Russell studied the formation as it is exposed along the North Fork of the Flathead River in British Columbia and adjacent Montana. Our work, starting in 1967, recovered additional vertebrates from Russell's locality E4 and led to our discovery of similar deposits farther south, within Glacier National Park, Montana. Later, we discovered Eocene vertebrates along the Middle Fork of the Flathead River. In the scarcity of badlands topography in this well forested region, the Middle Fork fossils were found primarily on cut-banks along that river and its tributaries (Fig. 5). Access to localities for prospecting was mostly via raft. Prospecting and sediment washing/screening produced a diversity of fossils, most of which are incomplete but range in size from very small (individual tooth length less than 1 mm, for some marsupials, insectivorans, rodents) to very large (tooth length 30–70 mm, for the amynodont rhinoceros and the brontotheres).

The radiometric date from deposits along the Middle Fork, the fauna of which occurs above the date of 46.2 $\pm$ 0.4 Ma, added to our interest in the fauna, thus assigned to the Bridgerian-Uintan NALMA. This interval has been the subject of a series of investigations involving North American mammalian faunas from the northern Great Plains (Uinta C of Swift Current Creek, Saskatchewan, Storer 1984), the Rocky Mountain region (Wagon Bed Formation, Badwater Creek area, Black and Dawson 1966; Tepee Trail Formation, Wiggins Formation, Eaton 1985; Tepee Trail Formation, Flynn 1986; Bridger and Uinta Basins, Gunnell et al. 2009); California (Walsh 1996a, b); and Texas (Whistler Squat, Devil's Graveyard, Campisano et al. 2012) that have led to increased understanding of the middle Eocene.

Many of the mammalian fossils discussed here from the Middle Fork exposures of the Kishenehn Formation consist of isolated dental and postcranial elements, mostly the former. Because of the lack of association of relevant parts of single animals, a relatively cautious approach is taken here on taxonomic assignments; those suggested may lack precision due to an incomplete record, pronounced individual variation within some taxa, and the fragmentary nature of many of the fossils. As a result, all the usual cautions about a record of this sort must apply (Beard and Dawson 2009).

The procedure followed here is to identify faunal elements as accurately as possible but not to assign each specimen to one taxon or another unless the record plausibly supports it. For the most part, attempts to associate more anterior teeth with molars were not undertaken. Some taxa can be most accurately identified if tooth sizes relative to one another can be ascertained, but in many cases this cannot be done on the basis of this Kishenehn record. Another potential difficulty is that for some mammals the parts represented by the fossils in question do not conform to the parts on which their identification is usually based. Among the brontotheres, for example, skull and especially horn morphology furnish most taxonomically utilized characters, but the Kishenehn's two brontothere taxa, based mostly on isolated teeth, do not permit use of such characters. Errors may have occurred in spite of a careful approach although it must be noted that mistaken taxonomic assignments can occur even with more complete samples (Walsh 1997). If an apparent taxon was very incompletely represented in the collections, its presence in the fauna may not have been reported.

Fossil localities (Table 2) occur along the banks of the Middle Fork and its tributary, Coal Creek. The most productive site, the Paola Rasmussen locality (M-28R), yielded numerous fossils to screen washing. In the same set of exposures, the Paola siding locality was also productive. Other localities, specified by M-numbers, were investigated by prospecting.

The early Uintan record for fossil mammals in the Kishenehn Formation contains a relatively low number of taxa, 26, compared to the later Uintan fauna from Swift Current Creek, from which 53 mammalian taxa have been identified although also by a relatively sparse number of individuals and completeness of representation (Storer 1996). A conservative approach has been chosen to avoid misleading range extensions and stratigraphic assignments, as much as possible. For some taxa, assignments given may be relatively uncertain. Some previous work has emphasized the difficulty of differentiating taxa based on such a record (Walsh 1997), even after presence of individual variation has been considered. Comparisons were made mostly with temporally relatively close faunas from the Rocky Mountain area, including those from Badwater and Tepee Trail, Wyoming, and the northern great plains, especially Swift Current Creek, Saskatchewan, as well as with Uintan faunas of Utah, southern California, and trans-Pecos Texas.

The non-vertebrate fossil record from the Middle Fork includes leaves, pollen, and mollusks (Pearce and Constenius 2014). Insects and spiders also are known from shale deposits in the lower Kishenehn deposits, including two new species of the Culicidae (mosquitoes), *Culiseta kishenehn* and *C. lemniscata* from paludal and lacustrine deposits of the middle part of the Coal Creek member, and the Hymenoptera *Eoeustochus kishenehn* and *E. borchersi* (Greenwalt and Constenius 2014; Greenwalt et al. 2015). Lower vertebrates including fishes (Li and Wilson 1994, for *Hiodon*; Liu et al. 2016, for *Amyzon* and amiids; note

TABLE 2			
Locality	Latitude	Longitude	Common Name
M-2	48.299183 N	113.606446 W	M2
M-3	48.303379 N	113.612440 W	M3
M-4	48.307919 N	113.610659 W	Park Creek -South
M-5	48.309770 N	113.612685 W	Park Creek -North
M-7	48.319574 N	113.627633 W	Kuhn's Point
M-9	48.327452 N	113.628595 W	Riverview Bend
M-28	48.386378 N	113.684951 W	Paola Siding
M-28R	48.386871 N	113.684400 W	Rasmussen bed
M-40T	48.422013 N	113.702309 W	Titanothera bed

that the correct Kishenehn fish locality should be exposures near Tunnel and Disbrow creeks in the Middle Fork Basin, not the South Fork Basin), and reptiles also occur, although relatively rarely. Scarce but non-diagnostic crocodilian teeth were found in the Middle Fork Paola Rasmussen washing site. Other reptiles are represented by osteoderms indicating presence of a glyptosaurine anguid. Chelonians are not common in the Kishenehn Middle Fork deposits although fragments of baenid support an age of Bridgerian or Uintan (Hutchison, personal communication). The Swift Current Creek Uintan has representatives of five chelonian families (Hutchison and Storer 1998) but no reported crocodilians.

Abbreviations used in the text are: ALMA, Asian Land Mammal Age; AMNH, vertebrate paleontology collections, American Museum of Natural History, New York; ar, argon; C, centigrade; CM, vertebrate paleontology collections, Carnegie Museum of Natural History, Pittsburgh; m, meter; mm, millimeter; MA, million years; NALMA, North American Land Mammal Age; NMC, Canadian Museum of Nature, Ottawa. Upper teeth are indicated by upper case letters, lower teeth by lower case. For teeth, a–p, greatest anteroposterior length; w, greatest transverse width; L, left side; R, right side; tal, talonid; tri, trigonid.

Small isolated teeth were measured using a Nikon SMZ 1500. One effect of this method is that the measurements tend to include more of the sides of the teeth than when made by measurements with calipers. The third decimal place in the measurements may not be accurate. Larger teeth were measured with Helios dial calipers. Scale bars on the figures are approximations so measurements with the descriptions are more accurate. For the most part higher taxonomic assignments follow usage from McKenna and Bell (1997) or Janis et al. (1998, 2008).

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Multituberculata Cope, 1884
Family Neoplagiulacidae Ameghino, 1890
Ectypodus Matthew and Granger, 1921

Ectypodus sp. cf. *Ectypodus lovei* (Sloan, 1966)
Fig. 6

Referred specimens.—CM 83106, Lm1; CM 83107, Lm1; CM 83108, Rm2; CM 83109, i1 or I1; CM 83110, LM1; CM 83112, RM1; CM 83113, LM2; CM 83114, RM2; CM 83115, fragmentary Rp4; CM 83116, fragmentary Lp4; CM 83117, Rm2; CM 83118, Rm2: locality M-28R.

Sample measurements.—CM 83106, Lm1, a–p 1.625 mm, w 0.965 mm; CM 83110, LM1, a–p 1.904 mm, w 1.056 mm; CM 83112, RM1, a–p 2.047 mm, w 1.080 mm. Cusp formula for m1, 6:4, m2, 3:2. Because neoplagiulacids are among the most difficult multituberculates to assign to lower taxa (Weil and Krause 2008), this species attribution is cautiously given. *Ectypodus lovei* was the first multituberculate to be recognized from post-Bridgerian time (Robinson et al. 1964). Geographically, the species has been found in Wyoming (Sloan 1966; Krishtalka and Black 1975), Nebraska (Ostrander 1984), North Dakota (Schumaker and Kihm 2006), Saskatchewan (Storer 1984), and Montana (this paper). A second species, *Ectypodus* sp., has been recorded from Duchesnean localities in Wyoming and Montana (Krishtalka and Black 1975), although Ostrander (1984) suggested that only one variable species is represented by these specimens, and Storer (1993) referred it to *Ectypodus lovei*. As currently recognized, *Ectypodus lovei* has a moderately long species range, middle Uintan to middle Chadronian (Krishtalka et al. 1982; Schumaker

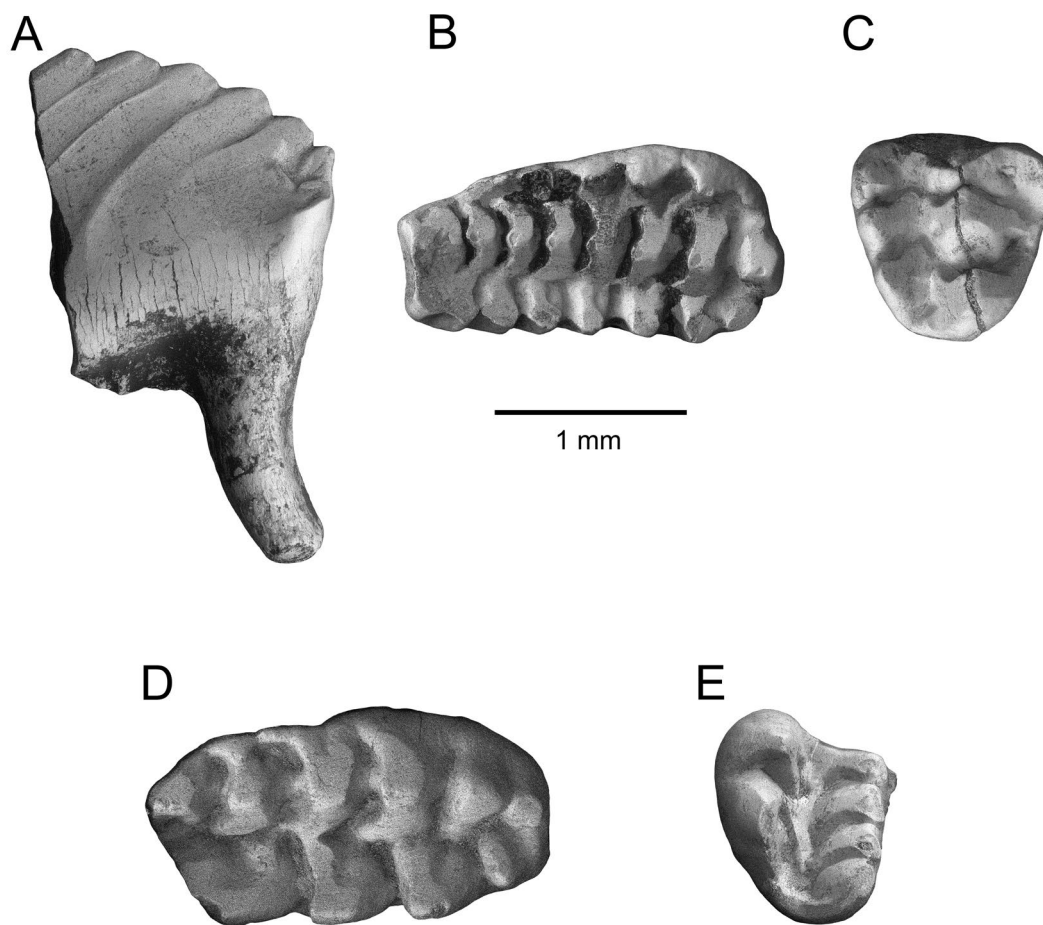


Fig. 6.—Multituberculata. *Ectypodus* sp. cf. *Ectypodus lovei*. **A**, CM 83115, incomplete Rp4; **B**, CM 83112, RM1; **C**, CM 83113, LM2; **D**, CM 83107, Lm1; **E**, CM 83117, Rm2.

and Kihm 2006). The Kishenehn occurrence appears to be its oldest. No multituberculata have been reported from the Californian or Texan Uintan-Duchesnean (Walsh 1996b; Campisano et al. 2014).

Fourteen isolated multituberculata cheek teeth are reported here from the Middle Fork deposits. The reference to *Ectypodus lovei* that is suggested for these teeth relates to the size range of the Badwater sample of that taxon (Krishtalka and Black 1975). It is also near the size of the Duchesnean *Ectypodus* sp. and Chadronian specimens of *Ectypodus lovei* (Schumaker and Kihm 2006). Only four multituberculata specimens, referred to *Ectypodus lovei*, were reported from the Swift Current Creek Uintan assemblage, their scarcity possibly related to loss of the smallest part of screened sediment during processing (Storer 1984).

The record of *Ectypodus* outside of North America includes the late Paleocene-early Eocene of Europe, where it presumably stemmed from a North American origin (Weil and Krause 2008), a premise supported by the most northerly occurrence of *Ectypodus*, *Ectypodus arctos* Beard and Dawson, 2014, in the Wasatchian of Arctic Canada.

Order Marsupialia Illiger, 1811
Family Didelphidae Gray, 1821

The record of marsupials in the Middle Fork deposits is based on 34 isolated molar teeth, and at least ten more anterior teeth, known entirely from the Paola Rasmussen screen washing locality. Two didelphid genera, a larger *Herpetotherium* Cope, 1873, and smaller *Peradectes* Matthew and Granger, 1921, appear to be represented. The former is more numerous.

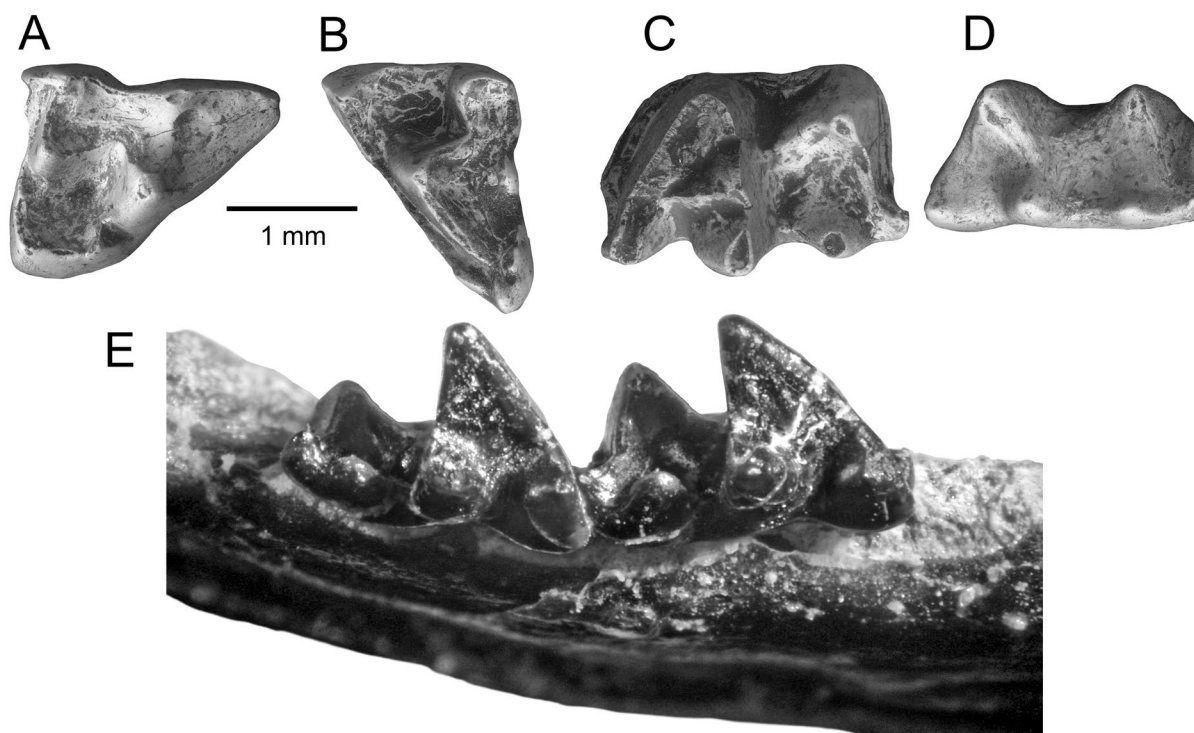


Fig. 7.—Marsupialia. *Herpetotherium* sp. cf. *Herpetotherium knighti*: A, CM 83380, LM1; B, CM 83386, LM4; C, CM 83392, Rm2 or 3. *Peradectes* sp. cf. *Peradectes californicus*: D, CM 83182, Rm. *Herpetotherium* sp. cf. *Herpetotherium knighti*: E, CM 83303, partial left mandible with m3-4.

Herpetotherium and *Peradectes* are both known from the Uintan to Duchesnean Badwater, Wyoming, localities (Setoguchi 1975; Krishtalka and Stucky 1983), where *Herpetotherium* cf. *Herpetotherium marsupium* (Troxell, 1923), *Herpetotherium innominatum* Simpson, 1928, *Herpetotherium* cf. *Herpetotherium knighti* McGrew, 1959, *Peradectes californicus* Stock, 1926, and *Peradectes* sp. cf. *Peradectes minutus* McGrew, 1937, were recorded. *Herpetotherium* has been reported also from Eocene localities in Saskatchewan (Storer 1984), Texas, California, and the Rocky Mountain area, and *Peradectes* from Saskatchewan, California, and the Rocky Mountain area (Walsh 1996a). Currently *Herpetotherium* is rare and *Peradectes* absent in the Uintan of the Uinta Basin. It has been suggested that species of *Herpetotherium* have long ranges, whereas those of *Peradectes* tend to be shorter (Krishtalka and Stucky 1983).

Subfamily Herpetotheriinae Trouessart, 1879
Herpetotherium Cope, 1873

Herpetotherium sp. cf. *Herpetotherium knighti*
 McGrew, 1959
 Figs. 7A–C, E

Referred specimens.—CM 83173, RM2; CM 83174,

RM4; CM 83175, Lm2; CM 83176, Lm2 or m3; CM 83177, Rm2 or m3; CM 83178, Lm1; CM 83179, LM2; CM 83180, Lp3?; CM 83303, L mandible with m3-4; CM 83380, LM1; CM 83381, RM1 or M2; CM 83382, RM1; CM 83383, LM2; CM 83384, RM2; CM 83385, LM1; CM 83386, LM4; CM 83387, Lm1; CM 83388, Rm1 or m2; CM 83389, Rm1 or m2; CM 83390, Rm2; CM 83391, Rm2 or m3; CM 83392, Rm2; CM 83393, Rm2 or m3; CM 83394, Rm2 or m3; CM 83395, LM4; CM 83396, LM2; CM 83397, LM2; CM 83398, LM2; CM 83399, RM4; plus unnumbered anterior teeth probably referable here: locality M-28R.

Sample measurements.—CM 83165, LM, a–p 1.988 mm, w 1.748 mm; CM 83380, LM, a–p 1.940 mm, w 1.995 mm; CM 83381, RM, a–p 1.913 mm, w 2.045 mm; CM 83386, LM4, a–p 1.460 mm, w 2.352 mm; CM 83389, Rm, a–p 2.137 mm, w 1.218 mm; CM 83392, Rm2, a–p 2.0894 mm, w 1.275 mm.

Herpetotherium knighti is a Wasatchian-Duchesnean taxon (Krishtalka and Stucky 1983) that appears to be the only representative of the genus in the Kishenehn Middle Fork localities, the identification here based mainly on size. Three species of *Herpetotherium* (as *Peratherium*) are reported from the Uintan fauna at Swift Current Creek (Storer 1984).

Subfamily Peradectinae Crochet, 1979
Peradectes Matthew and Granger, 1921

Peradectes sp. cf. *Peradectes californicus* (Stock, 1936)
 Fig. 7D

Referred specimens.—CM 83181, RM; CM 83182, Rm; CM 83183, LM; CM 83184, RM; CM 83185, RM; CM 83186, Rm3; CM 83187 Rm: locality M-28R.

Sample measurements.—CM 83181, RM, a–p 1.438 mm, w 1.808 mm; CM 83182, Rm, a–p 1.466 mm, w, 0.743 mm. CM 83187 may be a smaller taxon (RM, a–p 1.132 mm, w 0.732 mm) but is not taxonomically separated here from cf. *Peradectes californicus*.

Two species of *Peradectes*, *Peradectes californicus* and *Peradectes* cf. *Peradectes minutus*, are reported from the Uintan of Swift Current Creek (Storer 1996). The genus is reported to be geographically widely distributed (North and South America, Europe, Africa, McKenna and Bell 1997) but it is not clear whether this will be verified following close study.

Order Erinaceomorpha Gregory, 1910
 Family Erinaceidae Fischer von Waldheim, 1817

Erinaceid sp.

Referred specimens.—CM 83152–57, 83159, 83160, 83162 CM 83151, Lp4; CM 83152, RM; CM 83153, LM2; CM 83154, fragmentary L mandible with p4 and m1 trigonid; CM 83155, RM; CM 83156, Rm1; CM 83156, Rm1; CM 83157, Rm1; CM 83159, Rm1; CM 83160, LM; CM 83161, Rm3; CM 83162, Rm3: locality M-28R; CM 83158, Rm2: locality M-2; CM 83163, LM: locality M-28.

At least one erinaceid is represented by forty teeth in the Kishenehn deposits, providing a striking example of the difficulty of basing taxonomic evaluations solely on isolated teeth. Not only are the numerous erinaceid genera often poorly differentiated, but isolated teeth do not provide all of the critical evidence that is essential for associating anterior and more posterior teeth. An investigation of an erinaceid from the earliest Uintan (Shoshonean) of the Tepee Trail fauna of Wyoming (Flynn 1986), first mentioned forty years ago (Krishtalka and Setoguchi 1977), is now underway, based on well-preserved specimens from the AMNH collections. The Kishenehn erinaceid specimens do not appear referable to this still unnamed taxon.

Order Lipotyphla Haeckel, 1866
 Family Oligoryctidae Asher et al., 2002

Oligoryctes sp. Fig. 8

Referred specimens.—CM 83123, Rm1 or m2; CM 83124, fragmentary R mandible with p4 and partial m1;

CM 83125, Rm1 or m2; CM 83126, Lm1 or m2: locality M-28R.

Sample measurements.—CM 83125, Rm, a–p 1.084 mm, w 0.967 mm.

An obscure lipotyphlan is the tiny *Oligoryctes* Hough, 1956. Its presence in Uintan faunas such as Badwater and Swift Current Creek as well as in Uintan localities in California has done little to clarify its position in mammalian phylogeny. The Kishenehn lower molar (Fig. 8A) has a well-developed anterior cingulid, large trigonid, and very small, cusped talonid. It appears to be near the size of *Oligoryctes* sp. from Uintan localities at Badwater, Wyoming (Krishtalka and Setoguchi 1977). The genus *Oligoryctes* has been reported from the Bridgerian of the North American western interior (Asher et al. 2002). *Iconapternodus* Tong, 1997, and *?Apternodus* from the Irwin Manhan of China may be allied (Tong 1997).

Order Primates Linnaeus, 1758
 Family Omomyidae Trouessart, 1879
 Subfamily Omomyinae Trouessart, 1879
Stockia Gazin, 1958b

Stockia cf. *Stockia powayensis* Gazin, 1958b Fig. 9A

Referred specimens.—CM 83146 (right Rm2): locality M-2.

Sample measurements.—CM 83146, Rm2, a–p 2.839 mm, w 2.683 mm.

One right lower molar, complete except for slight wear or a small break at the tip of the entoconid, is the first North American record outside of California for the omomyid *Stockia*, where it is a part of the early Uintan Poway fauna in the Friars Formation (Gazin 1958b; Walsh 1996b). The very closely allied, or synonymous, *Asiomomys* Wang and Li, 1990, occurs in approximately Uintan-aged strata of Jilin, China (Beard and Wang 1991), with the species *Asiomomys changbaicus* Wang and Li, 1990. Other relationships of *Stockia* appear to be with the Bridgerian *Utahia kayi* Gazin, 1958b (Gazin 1958b; Honey 1990).

The rugose enamel that characterizes *Stockia powayensis* is clearly present in the Kishenehn primate, but is greater than in the Asian species. The hypoconulid is small. The assignment of *Stockia* to a species of *Omomys* Leidy, 1869, near the Bridgerian *Omomys carteri* Leidy, 1869 (Lillegraven 1980), was rejected by Honey (1990), Beard and Wang (1991), and McKenna and Bell (1997).

Asiomomys changbaicus is closer to *Stockia* than to any other Asian or European omomyid. Its source area at the Huadian locality in Jilin has been interpreted as having an equable climate due to maritime influences and to be a warm, moist, forested area at the Eocene time of deposition; oil shale and coal deposits in the region lend support to this interpretation (Beard and Wang 1991). Direction of

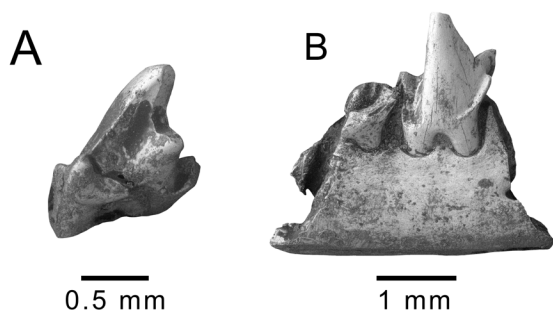


Fig. 8.—Oligoryctidae. *Oligoryctes* sp. A, CM 83125, Rm; B, CM 83124, right mandibular fragment with p4 and partial m1.

migration is considered to be from North America to Asia, based in part on the presence of the omomyid *Utahia* in the Bridgerian of North America.

The Kishenehn *Stockia* is near the size of the Poway specimens (Gazin 1958b) as well as *Asiomomys*. It does not resemble either of the two incompletely known species of omomyid from the Uintan of Swift Current Creek (Storer 1984), or *Omomys* sp. from the Duchesnean Lac Pelletier fauna (Storer 1990).

Subfamily Anaptomorphinae Cope, 1883

Trogolemur Matthew, 1909

Trogolemur sp. cf. *Trogolemur myodes* Matthew, 1909

Fig. 9B

Referred specimens.—CM 83119 small fragment of L mandible with m2: locality M-2.

Sample measurements.—CM 83119, Lm2, a–p 1.917 mm, w 1.594 mm.

The Kishenehn cf. *T. myodes* is in the size range of *T. myodes* from the early Bridgerian (Gazin 1958b) but larger than *T. myodes* from Elderberry Canyon, Nevada (Emry 1990). The trigonid is slightly narrower than the talonid. Paraconid and metaconid are lingual in position. A transverse metalophid connects protoconid and metaconid. The cristid obliqua extends mostly anteriorly and only slightly lingually from hypoconid to protoconid, and a second short lophid reaches from the hypoconid toward the talonid valley. The hypolophid curves buccally toward the posterior crest of the hypoconid. A narrow posterior cingulum occurs posterolingually.

Omomyids are rare at Swift Current Creek, where two omomyids, identified only to family, are reported on the basis of three specimens (Storer 1984), both of which are larger than the Kishenehn anaptomorphine. *Trogolemur leonardi* is reported from the Duchesnean Lac Pelletier lower fauna (Storer 1990), ?*Trogolemur* from Uintan Badwater locality 5a (Robinson 1968), *T. myodes* from the

Bridgerian Elderberry Canyon (Emry 1990), and cf. *T. myodes* from the Shoshonean Tepee Trail (Flynn 1986), yielding a generic age range from Bridgerian to Duchesnean. Only the omomyid *Ourayia* is reported from the Uintan Junction and Whistler Squat localities of Texas (Campisano et al. 2014).

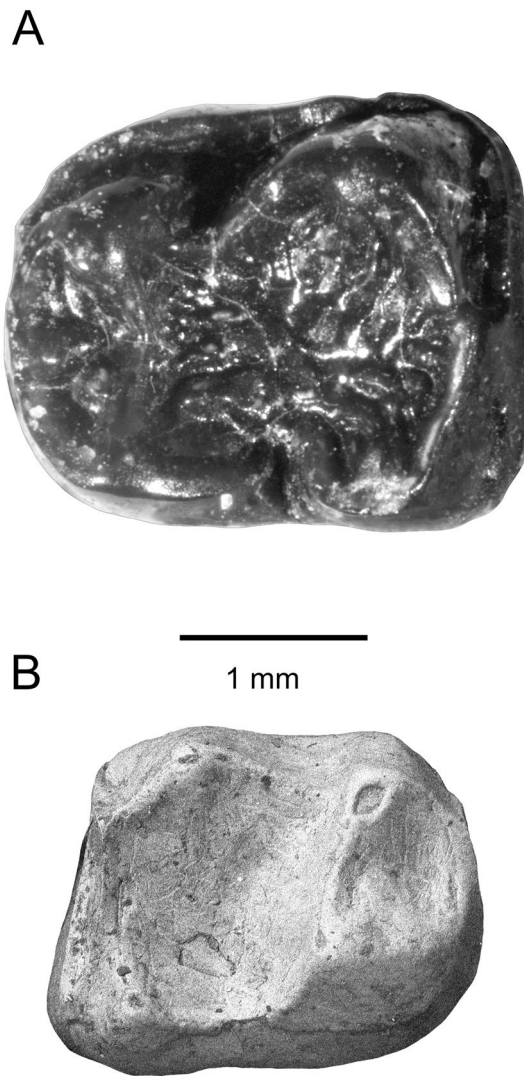


Fig. 9.—Omomyidae. A, *Stockia* cf. *S. powayensis*, CM 83146, Rm2. B, *Trogolemur* sp. cf. *T. myodes*, CM 83119, Lm2. Locality M-2.

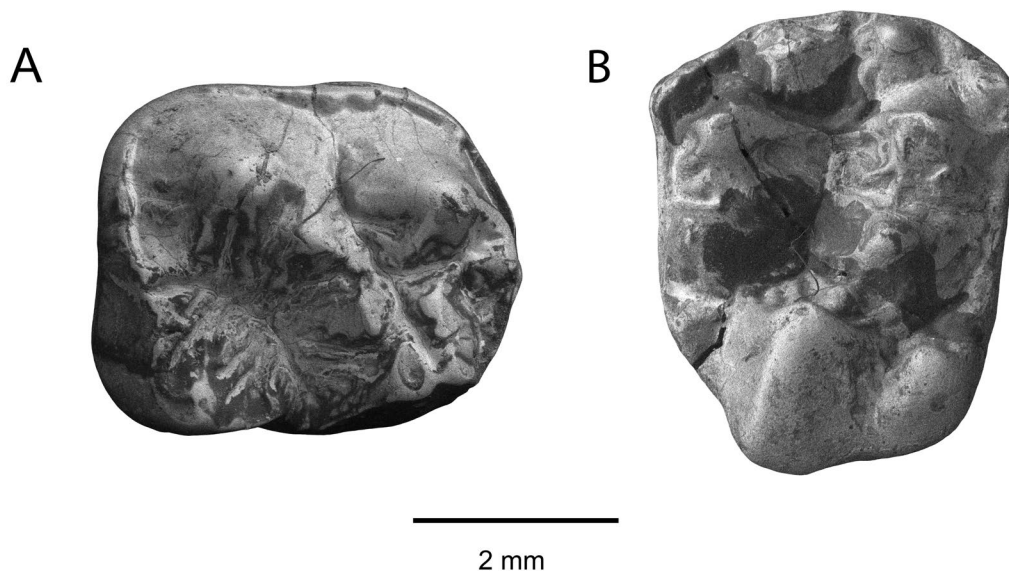


Fig. 10.—Omomyidae. *Tarkadectes montanensis*. A, CM 83111, Lm2; B, CM 82405, LM2.

Subfamily Tarkadectinae Szalay and Lucas, 1996

Tarkadectes McKenna, 1990

Tarkadectes montanensis McKenna, 1990

Fig. 10

Holotype.—CM 40818, fragmentary L mandible with p4–m2; locality M-28.

Referred specimens.—CM 82405, LM2; CM 83111, Lm2; CM 83137, Lm2; locality M-28R.

Sample measurements.—CM 82405, LM2, a–p 3.438 mm, w 4.493 mm; CM 83111, Lm2, a–p 4.002 mm, w 3.006 mm; CM 83137, Lm2, a–p 3.683 mm, w 3.330 mm.

The taxonomic history of *Tarkadectes* and its allies has been complicated, as might be expected in light of the relatively complex morphology and incomplete fossil record of the taxa involved. As first described (McKenna 1990; note that the Chadronian age given in that description is not valid, based on the incorrect radiometric dating at the time; see corrected date in introduction, above) the genera *Tarka* McKenna, 1990, and *Tarkadectes* were considered to be “plagiomenids (?Dermoptera).” The Tepee Trail environment from which *Tarka* was found has been referred to as a rarely sampled upland (McKenna 1990). Later, the Tarkadectinae was established for these genera as a new subfamily of Plagiomenidae (Szalay and Lucas 1996), based on *Tarkadectes*. The tarkadectines are characterized by a marked development of extra cusps on the upper and lower molars. Rose (2008) considered *Tarka* and *Tarkadectes* to be Plagiomenidae, whereas the first known

Asian tarkadectine *Tarkops* Ni et al., 2009, has been regarded as an omomyid primate (Ni et al. 2009), an attribution followed here.

Description.—The only currently known upper tooth of *Tarkadectes* is a nearly unworn left M2 (CM 82405, Fig. 10B) from the Paola Rasmussen locality. It is a distinctly cusped tooth, having two large, rounded cusps at the center of its slightly convex buccal side, flanked by parastyle and metastyle. A narrow ridge extends lingual from the more anterior of the styler cusps to terminate between the large paracone and metacone. More lingually situated paraconule and metaconule also are prominent. Posterior to the large protocone is a distinct conical hypocone. A small cuspule occupies a position in the lingual section on the anterior side of the tooth, which is slightly broken in this specimen. A narrow cingulum encircles posterior, buccal, and anterior sides of the tooth, with several small cuspules along its buccal side.

The type of *Tarkadectes montanensis*, CM 40818, left mandible with p4–m2 (McKenna 1990), has teeth that are somewhat more worn than this upper molar but still retain all their morphology. On p4 the cingulid crosses the anterior and buccal sides, and the talonid is reduced antero-posteriorly. On m1–2 the narrow cingulid crosses anterior, buccal, and posterior sides; small cuspules occur along the buccal cingulid of m1. The cristid obliqua has two small cuspules (centroconids of Ni et al. 2009) and a metastylid is adjacent to the metaconid. The entoconid is broken from m1 and there is an anterodorsal facing wear surface on m2. A small hypoconulid occupies part of the posterior

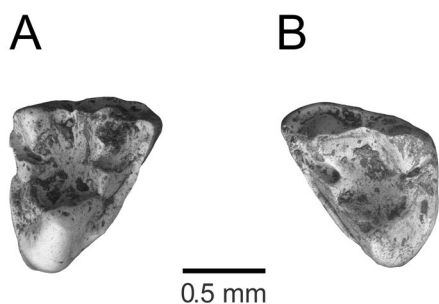


Fig. 11.—Microsyopidae, *Uintasorex* sp. cf. *U. parvulus*. **A**, CM 83306, LM3; **B**, CM 83307, RM.

cingulid. An unworn m2, CM 83111 (Fig. 10A), bears the wrinkled enamel characteristic of the genus as well as the posterolingual position of the small entoconid.

Tarkadectes exhibits a greater development of conules in the upper teeth than in *Tarka*. However, the former lacks the buccal cingular cusp that characterizes lower molars of both *Tarka* and *Tarkops*. *Ekgmowechashala* Macdonald, 1963, an early Arikareean primate that has been compared with tarkadectines, has a number of even more derived characters (Ni et al. 2009) but shares some other features, such as a well-developed hypocone, with *Tarkadectes*.

Anusha Ramdarshan (personal communication, 2014) determined that tooth wear indicated a folivorous diet for *Tarkadectes*. This deviates from McKenna's (1990) view that the diet of *Tarkadectes* emphasized fruits, insects, gum, and sap, although with more fibrous food than *Tarka*.

Tarkadectines are currently known from northern parts of the Rocky Mountain region and eastern Asia; it is a likely intercontinental immigrant. The middle Eocene (Irdin Manhan ALMA) *Tarkops mckennai* Ni et al., 2009, of Inner Mongolia has been considered more primitive than *Tarka* and possibly older than earliest Uintan (Ni et al. 2009). Accordingly, its direction of migration can be suggested as being from Asia to North America.

Order Plesiadapiformes Simons and Tattersall, 1972
Family Microsyopidae Osborn and Wortman, 1892
Subfamily Uintasoricinae Szalay, 1969

Uintasorex sp. cf. *Uintasorex parvulus* Matthew, 1909
Fig. 11

Referred specimens.—CM 83304, Rp4; CM 83305, LM; CM 83306, LM3; CM 83307, RM: locality M-28R.

Sample measurements.—CM 83305, LM1 or 2, a–p 0.924 mm, w 1.233 mm; CM 83306, LM3, a–p 0.870 mm, w 1.211 mm.

Four teeth of the tiny plesiadapiform *Uintasorex* Matthew, 1909, were recovered by screen washing at the Kishenehn Paola Rasmussen locality. Robinson (1968) referred to the Uintan specimens from Badwater, Wyoming, as *Uintasorex* sp. cf. *U. parvulus*, adding that they are very similar to Bridgerian *Uintasorex*; at that time this was an upward time range extension for the taxon. The Kishenehn *Uintasorex* is larger than the Badwater specimens and more similar in size range to those from the Bridgerian of Powder Wash, Utah (Szalay 1969).

The genus is known also from the Bridgerian to Uintan of Wyoming, Uintan of California (Mission Valley and Friars formations, Lillegraven 1976), and Duchesnean of Lac Pelletier lower and upper faunas of Saskatchewan (Storer 1996); the last is regarded by Storer (1995) as the latest then known occurrence of *Uintasorex*.

Order Lagomorpha Brandt, 1855
Family Leporidae Fischer von Waldheim, 1817

Leporid indet.
Fig. 12

Referred specimens.—CM 83308, partial LdP4; CM 83309, Rdp4: locality M-28R.

Sample measurements.—CM 83308, partial LdP4, a–p 1.682 mm, w 2.412 mm; CM 83309, Rdp4, a–p 2.079 mm, w 1.490 mm.

Two deciduous premolars, relatively low crowned, and probably representing one taxon, are the sole record of lagomorphs in the Kishenehn Middle Fork deposits.

While leporids appear to have been relatively recent Uintan migrants into North America, they are well represented in later Uintan localities in the Rocky Mountain area, including *Mytonolagus* Burke, 1934, in the Myton member of the Uinta Formation, Utah (Burke 1934), and

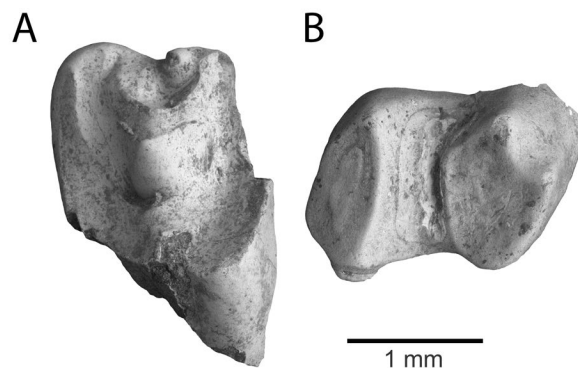


Fig. 12.—Leporid indet. **A**, CM 83308, partial LdP4; **B**, CM 83309, Rdp4.

in the Wagon Bed Formation at Badwater, Wyoming (Dawson 1970). The sparse record in the Kishenehn deposits may be, however, the oldest record for lagomorphs in North America. Lagomorphs are rare in the late Uintan or Duchesnean Laguna Riviera of California (Walsh 1996b), and absent in the Eocene of Texas. The Kishenehn record differs strongly from that of Swift Current Creek, Saskatchewan, which has yielded the relatively abundant leporid *Procaprolagus* Gureev, 1960, and a second, undetermined leporid (Storer 1984).

Order Rodentia Bowdich, 1821

Although several Kishenehn Middle Fork Uintan taxa are rodents, their remains consist almost entirely of isolated teeth. Rodent identification is subject to the usual difficulties for ascertaining tooth associations and defining characteristics, simplified only by having reduced the number of teeth present in a full adult dentition. The problem is acute for the ischyromyids (paramyids), relatively primitive and homogeneous rodents having few unique cheek tooth characters (Wood 1962). In the absence of associated evidence on such characters as incisor morphology and skull structure, including the zygomatic region, identifications can be especially problematic. Rodents are well represented in most North American localities preserving the Uintan, which was a time of their increasing family-level diversification. Ischyromyids including microparamyines, a sciuravid, and an eomyid are represented in the Middle Fork fauna. Absence of cylindrodontid rodents is a striking feature of the fauna, presumably environmentally related. Although cylindrodontids occur in many Eocene localities, they are absent as well at the Bridgerian Elderberry Canyon locality of Nevada, which contains the rodents *Reithroparamys delicatissimus* Leidy, 1871, *Reithroparamys* cf. *R. huerfanensis* Wood, 1962, *Microparamys sambucus* Korth and Emry, 1989, ischyromyid sp. indet., *Sciuravus* sp., *Pauromys exallos* Korth and Emry, 1989, *Knightomys* sp., *Elymys complexus* Korth and Emry, 1989, and *Matimys* sp. (Emry and Korth, 1989).

Numerically, the Middle Fork fossil rodent record is dominated by eomyids, tiny rodents having tooth lengths in the <1 mm size range, all retrieved from the Paola Rasmussen screen washing locality. Walsh (1997) demonstrated how several Eocene rodent genera including *Pauromys* Troxell, 1923, and *Sciuravus* Marsh, 1871, were mixed into the generic description of the eomyid *Metanoiamys*, discussed the problems inherent in taxonomic assignments for isolated rodent teeth, and showed how individuals of various species within these genera have previously been subject to generic misidentification. This caution must be applied also to some of the isolated teeth discussed here that may actually represent the eomyid or the small sciuravid *Pauromys*.

Differences in composition of the rodent faunas become apparent in comparisons with the Uintan-Duchesnean

Badwater, Wyoming, and Uintan Swift Current Creek, Saskatchewan, faunas, both of which have greater rodent diversity than the Middle Fork Kishenehn. Badwater rodents, while not completely described, include at least nine species of ischyromyids including two prosciurines, plus four species of cylindrodontids, one of sciuravid and one of eomyid. The Swift Current Creek Uintan has three species of ischyromyids plus two species of microparamyines, as well as an ?eutypomyid, *Pseudocylindrodon* Burke, 1935, *Janimus mirus* Storer, 1984, eomyids (*Protadjidaumo* Burke, 1934, *Metanoiamys*), and a prosciurine. The Texas Uintan Whistler Squat locality has yielded two ischyromyid taxa plus a microparamyine, one cylindrodontid and two sciuravids, *Sciuravus* and *Pauromys* (Walsh 1997, questioned some of the latter identifications).

Family Ischyromyidae Alston, 1876

The ischyromyids are moderately diverse rodents in the Middle Fork fauna, with at least four taxa of ischyromyids based on 15 isolated teeth, plus two microparamyine taxa. The suggested taxonomic determinations for these rodents are far from precise, based mostly on reasonable size associations; those of upper and lower teeth are less clear and must remain relatively insecure. Having four ischyromyid taxa is the Texas Uintan Whistler Squat locality; five occur in the Uintan at Swift Current Creek; nine are reported in the longer lasting (Uintan-Duchesnean) Badwater localities; and nine in the Elderberry Canyon Bridgerian. The occurrence of six taxa of Kishenehn ischyromyids is not excessive. No attempt was made to associate deciduous with permanent teeth.

Outside of size differences, there are many similarities among the larger Kishenehn ischyromyids, all of which have relatively simple molar patterns with para- and meta- on the upper molars converging toward the protocone, a pattern that also characterizes the middle Eocene (Irdin Manhan) Asian rodent *Asiomys* Qi, 1987 (Liu and Meng 2013). *Asiomys* is more similar to North American than to Asian ischyromyids, adding another piece as evidence for vertebrate exchanges between Asia and North America during the middle Eocene. *Asiomys* has double metaconules on the upper molars, which occurs also in Kishenehn ischyromyid 3, CM 83171, as do the hypoconid connected to posterolophid, ectolophid complete, enamel on posteroloph and posterolophid wrinkled.

Ischyromyid 1

Referred specimen.—CM 83379, Lp4: locality M-2.

Sample measurements.—CM 83379, Lp4, a–p 4.518 mm, w 4.835 mm.

The primary character considered here is size. CM 83379, left p4, is a well-worn tooth of the largest ischyromyid represented; most of the occlusal pattern of the

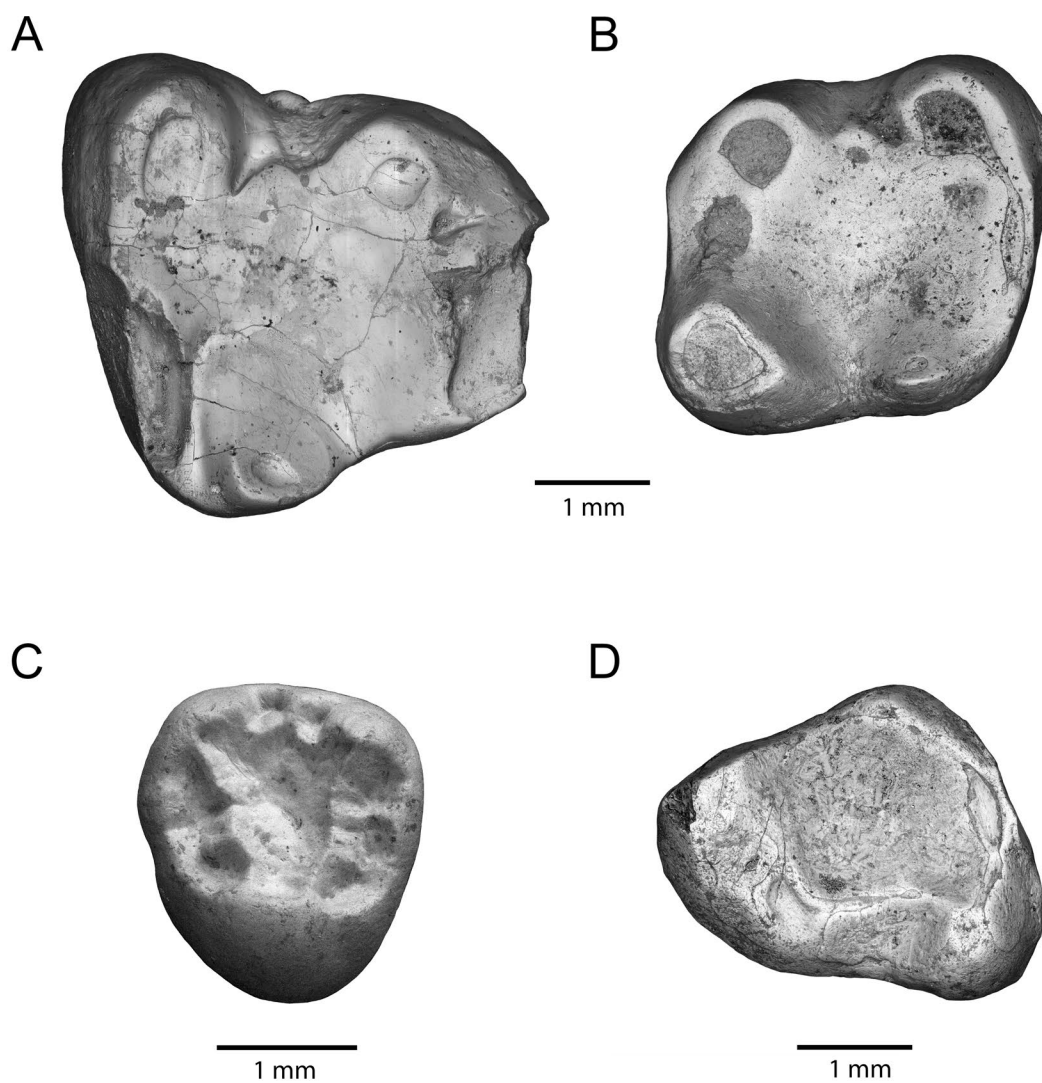


Fig. 13.—Ischyromyid spp. **A**, ischyromyid 2, CM 83299, Lp4; **B**, ischyromyid 3, CM 83169, Rm; **C**, ischyromyid 4, near *Thisbemys corrugatus*, CM 83132, Lm; **D**, CM 83166, Lp4.

tooth is worn away, leaving a small mesoconid, metaconid elongated toward protoconid by a short metalophid, large rounded entoconid and wide talonid. Large size sets it apart from the other Kishenehn ischyromyids but the incomplete record indicates that affinities outside of familial must remain uncertain.

Ischyromyid 2

Fig. 13A

Referred specimens.—CM 83164, Lp4: locality M-28R; CM 83138, Lp4; CM 83300, LM; CM 83301, LM2; CM 83302, Lm1: locality M-2.

Sample measurements.—CM 83299, Lp4, broken anteriorly, w 3.889 mm; CM 83300, LM, a-p 3.685 mm, w 4.386 mm.

The upper molar, CM 83300, is a large cusate tooth; the protocone is centrally located on the lingual side, somewhat as in *Ischyrotomus* Matthew, 1910, and *Pseudotomus* Cope, 1872, and is flanked anteriorly by the cusate lingual end of the anterior cingulum and posteriorly by the small rounded hypocone; the metaloph is oriented toward the protocone. A narrow loph extends from the paracone toward the anterior side of the protocone with a small protoconule; the metacone is large, rounded, and also oriented toward the protocone. There is no ectoloph but a small rounded mesostyle occurs on the buccal side between paracone and metacone. The enamel of the lingual wall of the upper molar is distinctly wrinkled. The possibly associated p4 (Fig. 13A) is a cusate tooth, having a distinct entoconid, a small anteriorly directed cuspule between protoconid and metaconid, complete ectolophid with a small mesoconid, and a well-developed posterior cingulid. Note that little confidence should be placed on the association of upper and lower teeth.

Ischyromyid 3

Fig. 13B

Referred specimens.—CM 83169, Lm1 or: locality M-2; CM 83170, LM; CM 83171, RM1 or M2: locality M-28R.

Sample measurements.—CM 83169, Lm1 or m2, a-p 3.399 mm, w 3.572 mm; CM 83171, RM1 or M2, a-p 3.318 mm, w 4.113 mm.

These three teeth are relatively simple, which may be appropriate for association on the basis of size. The upper molar, CM 83171, has protoconule and metaconule but a relatively simple pattern. The double metaconule resembles that of *Asiomys*.

Ischyromyid 4, near *Thisbemys corrugatus* Wood, 1959
Figs. 13C–D

Referred specimens.—CM 83132, LM3; CM 83166,

Lp4; CM 92813, Lp4: locality M-28R.

Sample measurements.—CM 83132, LM, a-p 3.205 mm, w 3.387 mm; CM 83166, Lp4, a-p 3.040 mm, w 2.939 mm. These two teeth are here associated basically on size. The M3, CM 83132, has considerable complexity of pattern with a distinct mesostyle, well-developed hypocone, large, elongated protoconule and metaconule, but the metacone is not prominent. Suggested affinity with *Thisbemys* Wood, 1959, is based largely on this complexity. The p4 has wrinkled enamel in the central basin.

Subfamily Microparamyinae Wood, 1962

As *Microparamys* Wood, 1959, is currently recognized, its numerous species present both a wide geographic distribution (Rocky Mountain area, Nevada-California, Texas, Saskatchewan, Ellesmere Island, western Europe) and a moderately long stratigraphic record (late Paleocene Clarkforkian through late Eocene Chadronian). North American mid-latitude species, in approximate stratigraphic order, oldest to youngest, are: *M. cheradius* Ivy, 1990 (Clarkforkian-Wasatchian); *M. hunterae* Ivy, 1990, *M. bayi* Dawson, 2001, *M. regisylvestris* Dawson, 2006, *M. scopaiodon* Korth, 1984 (Wasatchian); *M. minutus* Wilson, 1937, *M. sambucus* (Bridgerian); *M. dubius* Wood, 1949, *M. woodi* Kelly and Whistler, 1994, *M. solidus* Storer, 1984 (Uintan); *M. tricus* Wilson, 1940, *M. nimius* Storer, 1988 (Duchesnean); *M. perfossus* Wood, 1974 (Chadronian). Closely allied microparamyines include *Strathcona major* Dawson, 2001, and *Strathcona minor* Dawson, 2001 (Wasatchian), both Arctic taxa (Dawson 2001). *Churcheria baroni* Storer, 1988 (Duchesnean of Saskatchewan, Storer 1988) may also be allied. The European microparamyines (Escarguel 1999) include early and middle Eocene *Microparamys* (sp., *M. nanus* Teilhard de Jardin, 1927, *M. hottingeri* Marandot, 1989, *M. paisi* Estravis, 1994), *Sparnacomyss* Hartenberger, 1971 (1 sp.), *Pantrogna* Hartenberger, 1971 (2 sp.), *Hartenbergeromys* Escarguel, 1999 (2 sp.), and *Masillamys* Tobien, 1954 (2 sp.). The extant rodent family Gliridae stems from European microparamyines (Thaler 1966; Hartenberger 1971).

The Kishenehn species of *Microparamys* were collected from the Paola Rasmussen screen-washing locality (M-28 R), M-2, and Coal Creek. As much as screen washing has added to the fossil record, especially for the smaller and frequently rarer elements of an assemblage, use of the isolated teeth that usually compose the faunal elements from screen washing does not provide an unequivocal record. Among the rodents, for example, confusion of teeth from such diverse taxa as *Microparamys*, *Pauromys*, and primitive eomyids, including *Metanoiamys*, can frequently lead to incorrect taxonomic assignments (Walsh 1997).

No Asian occurrence has been reported for microparamyines.

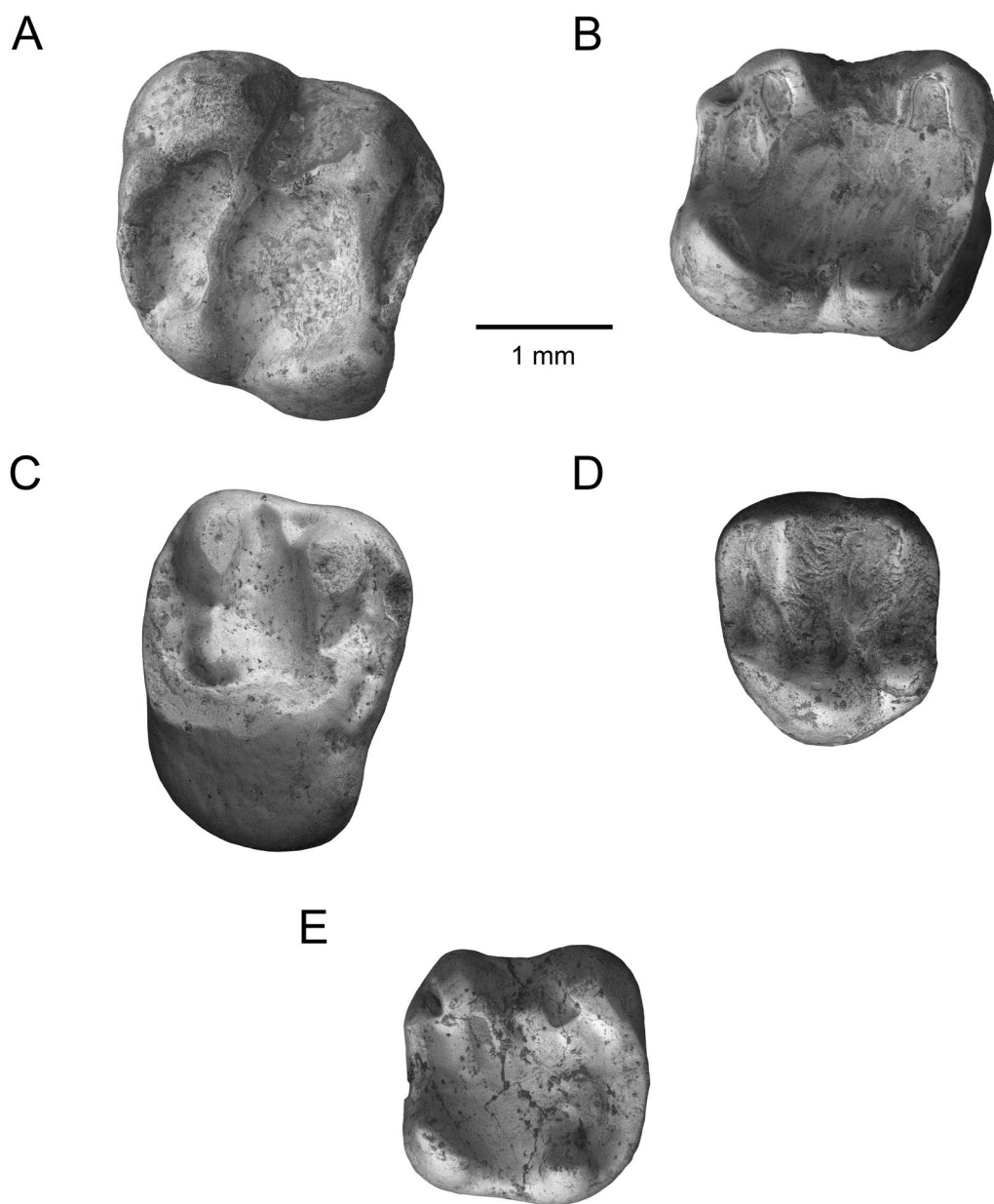


Fig. 14.—*Microparamys solis*, new species, A-C. **A**, holotype, CM 83102, Lm3; **B**, CM 83103, Rm; **C**, CM 83134, RM. *Microparamys* near *M. sambucus*, D-E. **D**, CM 92801, LM1; **E**, CM 92800, Rm2.

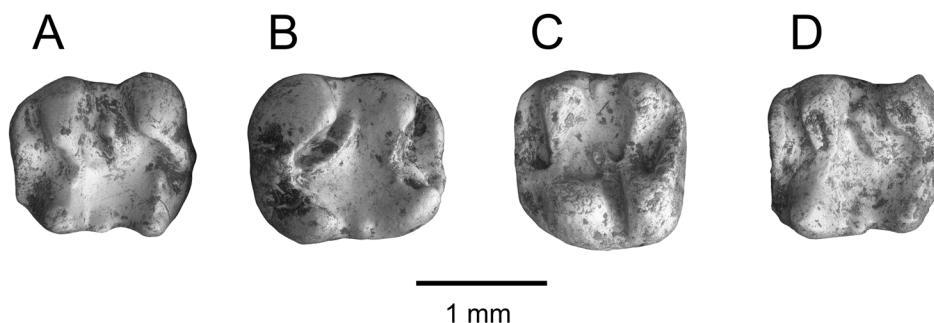


Fig. 15.—*Pauromys* sp. near *P. lillegraveni*. **A**, CM 83190, Rm; **B**, CM 83192, Lm3; **C**, CM 83195, LM; **D**, CM 83196, Rm.

***Microparamys solis*, new species**

Figs. 14A–C

Holotype.—CM 83102, Lm3: locality M-28R.

Referred specimens.—CM 83101, Rm: locality M-2; CM 83100, LM1 or M2; CM 83103, Rm; CM 83104, Rm; CM 83105, Lm; CM 83129, RM3; CM 83130, Rp4; CM 83131, Lp4; CM 83133, LM3; CM 83134, Rm; CM 83135, Rm; CM 92806, RM3; CM 92907, RP4; CM 92808, RM; CM 92809, RM; CM 92810, LM; CM 92811, Lm3; CM 92812, Lm: locality M-28R; CM 83139, Ldp4 or Lp4: locality M-40T.

Sample measurements.—CM 83102, Lm3, a–p 2.121 mm, w 2.293 mm; CM 83103, Rm, a–p 2.221 mm, w 2.341 mm; CM 83104, Rm, a–p 2.202 mm, w 2.277 mm; CM 83105, Lm, a–p 2.147 mm, w 2.491 mm; CM 83129, RM3, a–p 2.043 mm, w 2.119 mm; CM 83130, Rp4, a–p 2.294 mm, w 2.295 mm; CM 83131, Lp4, a–p 1.844 mm, w 2.341 mm; CM 92806, RM3, a–p 1.774 mm, w 1.909 mm; CM 92809, RM, a–p 1.978 mm, w 2.006 mm; CM 92811, Lm3, a–p 2.059 mm, w 1.973 mm.

Diagnosis.—Large-sized *Microparamys*, slightly larger than Californian *M. tricus* (Sespe loc. 150, Pearson Ranch, Duchesnean). Small but distinct hypocone on upper molars, metaconule-metaloph directed toward protocone. Well-developed transverse lophids in lower molars, including anterior cingulid separated buccally from protoconid. The holotype, CM 83102, Lm3, shows that the metalophid extends to the anterior side of the metaconid and is well developed to the protoconid; the mesoconid is crowded next to the ectolophid; there is a well-developed hypolophid and a prominent cingulid with a rounded hypoconulid; the enamel is lightly crenulated in the basins.

Etymology.—Latin, *sol* (sun), named with thanks to

CMNH librarian Xianghua Sun.

Seven upper and ten lower cheek teeth represent a species of *Microparamys* that is larger than is often found in this genus, although smaller than the size range of *M. solidus* of Swift Current Creek (Storer 1984). The lower molars have transverse lophs and a well-developed anterior cingulid that is separated buccally, in early wear stages, from the protoconid, a metalophid between the metaconid and protoconid, and a narrow hypolophid between the hypoconid and entoconid. A small mesoconid is on the ectolophid in the buccal exit of the central basin. A small, rounded metastylid is variably present, posterior to the metalophid. The prominent posterior cingulid has a distinct, rounded hypoconulid. Enamel in the relatively unworn basins of CM 83102 is coarsely wrinkled.

The Californian species *M. tricus* is large (Wilson 1940), but it is exceeded by the Kishenehn and Swift Current Creek species, as well as by some of the Arctic microparamyines (Dawson 2001). *Microparamys solis* is near the size of the Arctic Wasatchian *Strathcona major*. European members of the genus tend toward small size (Escarguel 1999), which also characterizes many of the North American species.

Microparamys* sp. near *Microparamys sambucus

Korth and Emry, 1989

Figs. 14D–E

Referred specimens.—CM 92800, Rm2; CM 92801, LM1 or M2; CM 92802, RM; CM 92804, Lm3; CM 92805, LM1, locality M-28R; CM 92803, Lm3: locality 40-T.

Sample measurements.—CM 92801, LM1 or LM2, a–p 1.242 mm, w 1.381 mm; CM 92800, Rm2, a–p 1.390 mm, w 1.447 mm; CM 92803, Lm3, a–p, 0.983 mm, w 0.965 mm.

While in the size range of the Uintan-Duchesnean

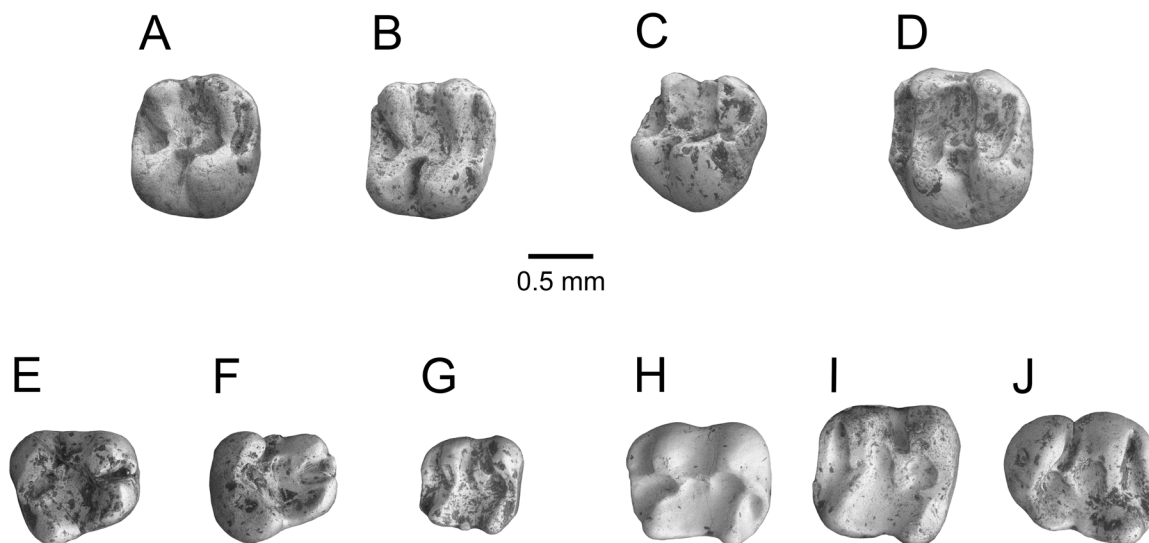


Fig. 16.—Eomyidae. cf. *Metanoiamys* sp. A–D, upper cheek teeth: **A**, CM 83329, RM; **B**, CM 83330, RM; **C**, CM 83344, RM3; **D**, CM 83350, LM3; E–J, lower cheek teeth: **E**, CM 83310, Lp4; **F**, CM 83317, Lp4; **G**, CM 83319, Rp4; **H**, CM 83313, Rm; **I**, CM 83321 Rm; **J**, CM 83320, Lm3.

M. dubius, this Kishenehn rodent appears to be a different species. It is similar to the slightly larger Elderberry Canyon *M. sambucus* in having a weak central region of the hypolophid (Emry and Korth 1989), a character in which it differs from *M. dubius*. The posterior arm of the protoconid is short, and the transverse metalophid extends into the anterior cingulid, similar to the structures in *M. tricus* and *M. minutus*. A small mesoconid, metastylid, and hypoconulid are present.

Family Sciuravidae Miller and Gidley, 1918
Pauromys Troxell, 1923

Pauromys sp. near *Pauromys lillegraveni* Walsh, 1997
Fig. 15

Referred specimens.—CM 83168, LM; CM 83197, Rm; CM 83188, Rm; CM 83190, Rm1 or m2: locality M-28R

Sample measurements.—CM 83190, Rm, a–p 1.129 mm, w 0.965 mm; CM 83195, LM, a–p 1.031 mm, w 1.115 mm.

This North American rodent, which is characterized by

loss of P3 and reduced size of P4/p4, ranges through the Bridgerian and early Uintan. Geographically, the genus is widely distributed, having been reported, north to south, from Montana and Wyoming to Texas, and, east-west, through localities in Utah and Nevada to California. It is not recorded from the Uintan or Duchesnean of Saskatchewan (Storer 1996). Not all references of species to *Pauromys* have been accepted, although *P. perditus* Troxell, 1923 (Bridger Basin, Wyoming), *Pauromys* sp. (Powder Wash, Utah), and *P. lillegraveni* (California) are recognized in the most recent relevant evaluation of its taxonomy (Walsh 1997). In that study, the genus is regarded as a primitive member of the Myodonta, slightly more derived than *Armitomys* Dawson et al., 1990, an attribution not followed here. *Pauromys* sp. from the Lost Cabinian of Wyoming (Korth 1984) is too incompletely known for a definite reference to the genus. The oldest Uintan record of *Pauromys* appears to be in the Turtle Bluff Member, U1a biochron (Gunnell et al. 2009). One tooth has been referred to *P. texensis* Walton, 1993, from the U1l Whistler Squat fauna, Devil's Graveyard Formation, Texas (Campisano et al. 2014), although the species identification of this taxon

had previously been questioned by Walsh (1997), who also postulated that the specimens described by Walton (1993) as *P. texensis* may pertain to the eomyid *Metanoiamys*.

Pauromys lillegraveni, which stems originally from the late early Uintan Stadium Conglomerate of San Diego County, California, has a weak, transversely compressed metastylid at the posterior end of the lingual lophid from the metaconid (Walsh 1997), a character shared by the Kishenehn *Pauromys*, for which size also is in agreement; on upper molars a small mesostyle is present. Another species of *Pauromys*, *P. exallos* Emry and Korth, 1989, from the early Bridgerian Elderberry Canyon fauna of Nevada (Emry and Korth 1989), shares important characters with this Kishenehn rodent, including such distinctive morphological features of the cusps and lophs as an anterobuccally directed lophule into the central valley of M1–2, and a transversely elongated mesolophid that curves posteriorly on m3. However, the Kishenehn *Pauromys* differs from *P. exallos* in being smaller and in having a distinct metastylid on the lower molars. Walsh (1997) questioned the assignment of *P. exallos* to *Pauromys* and regarded the Texan *P. texensis* and *P. simplex* Walton, 1993, as referable to genera other than *Pauromys*. Kishenehn specimens of this small rodent genus are near the size of Bridgerian *Pauromys* sp. from Powder Wash, Utah (Dawson 1968) as well as *P. lillegraveni*. The Kishenehn *Pauromys* differs from *Pauromys* sp. and from Bridgerian species *P. perditus*, *P. schaubi* Wood, 1959, and *P. exallos* in having a well-defined metastylid on the lower molars, also present in *P. lillegraveni* (Walsh 1997). The upper molars have a well-developed anterior cingulum, a short loph from the hypocone into the central valley, a small mesostyle buccally between the paracone and the metacone, a complete hypoloph connecting metacone and hypocone, and a small gap between the posterior cingulum and metacone. Lower molars have a well-developed anterior cingulid, a metalophid between the protoconid and metaconid, the ectolophid is absent, a short mesolophid extends posterolingually from the buccal valley into the central valley, a rounded metastylid on the lingual ridge extending posteriorly from the metalophid, and some development of a lophid extending buccally from the entoconid toward the hypoconid except on m3 in which there is instead a distinct wide posterior cingulid.

Metanoiamys and *Pauromys* also occur together in the Turtle Bluff member U1a biochron (Gunnell et al. 2009). No larger sciuravid species are known from the Kishenehn Uintan deposits.

Family Eomyidae

Eomyid cf. *Metanoiamys* sp.

Fig. 16

Referred specimens.—CM 83310, Lp4; CM 83311, Rm3; CM 83312, Lm3; CM 83313, Rm; CM 83314, Rm3; CM 83315, LM; CM 83316, Rp4; CM 83317, Lp4; CM 83318, Lm1 or m2; CM 83319, Rp4; CM 83320, Lm3;

CM 83321, Rm2; CM 83322, Rm; CM 83323, Lm; CM 83324, Lm2; CM 83325, Rm; CM 83326, Rm; CM 83327, Rm; CM 83328, Rm3; CM 83329, RM1 or M2; CM 83330, RM; CM 83331, LM1 or M2; CM 83332, LM; CM 83333, RM1 or M2; CM 83334, RM; CM 83335, RM; CM 83336, ?RM3; CM 83337, LM1 or M2; CM 83338, LM; CM 83339, RM1 or M2; CM 83340, RM; CM 83341, LM1 or M2; CM 83342, RM1 or M2; CM 83343, RM1 or M2; CM 83344, RM3; CM 83345, Rm; CM 83346, LP; CM 83347, RM; CM 83348, RM; CM 83349, RM; CM 83350, LM3; CM 83374, Rm; CM 83375, Rp4; CM 83376, Rm; CM 83377, Rm3; CM 83378, RM; CM 92814, RM; CM 92815, Rm; CM 92816, RM; CM 92817, Rm1 or m2; CM 92818, m; CM 92819, m; CM 92820, Lp4; CM 92821, Lp4; CM 92822, broken RM; CM 92823, Rm; CM 92824, Rm; CM 92825, Rm3; CM 92826, Rm3; CM 92827, Lm locality M-28R.

Sample measurements.—CM 83310, Lp4, a–p 0.845 mm, w 0.831 mm; CM 83313, Rm, a–p 0.945 mm, w 0.850 mm; CM 83314, Rm3, a–p 0.914 mm, w 0.879 mm.

By count of the isolated teeth referred here, this small rodent is the most abundantly represented mammal in the Middle Fork assemblage, more than 40 of its isolated teeth being known from the Paola Rasmussen screen washing site. Eomyid affinities of this rodent are suggested by a number of characters including the well-developed quadrate shape of P4. Unfortunately, this record does not reveal evidence on its skull structure, which for middle Eocene eomyids remains unknown whether it was sciurognathous, as are later eomyids, or primitively protrogomorphous (Wilson 1949; Wahlert 1978; Korth et al. 2015). Walsh (1997) demonstrated that the mandible of the early eomyid *Metanoiamys* is sciurognathous, reviewed the record of the taxon in the Eocene of California, as well as the records of *Pauromys* and *Simimys* Wilson, 1935, and clearly demonstrated the problems inherent in interpreting isolated teeth of small rodents. He proposed various synonymies among Uintan-Duchesnean species of *Metanoiamys*, *Pauromys*, and *Microparamys*, and pointed out that *Metanoiamys* appears to have the ancestral eomyid morphotype with P4 and p4 smaller relative to M1 and m1 than in later eomyids, in which the premolars become larger. It may be accepted that, based on currently available evidence, eomyids are derived from North American sciuravids, although “considering the entire Holarctic radiation of the family, there is little consensus regarding systematics below the family level for Eomyidae” (Flynn 2008:416). *Metanoiamys* also occurs with a Bridgerian aspect assemblage including *Mysops* Leidy, 1871, *Pauromys*, and *Microparamys* in the Turtle Bluff member in the U1a biochron (Gunnell et al. 2009).

Comparisons of the small Kishenehn eomyid with other *Metanoiamys*, which range from early Uintan through Chadronian (Chiment and Korth 1996; Kelly 2010; Emry and Korth 2012), and has species including *Metanoiamys fantasma* Lindsay, 1968, *Metanoiamys fugitivus* Storer,

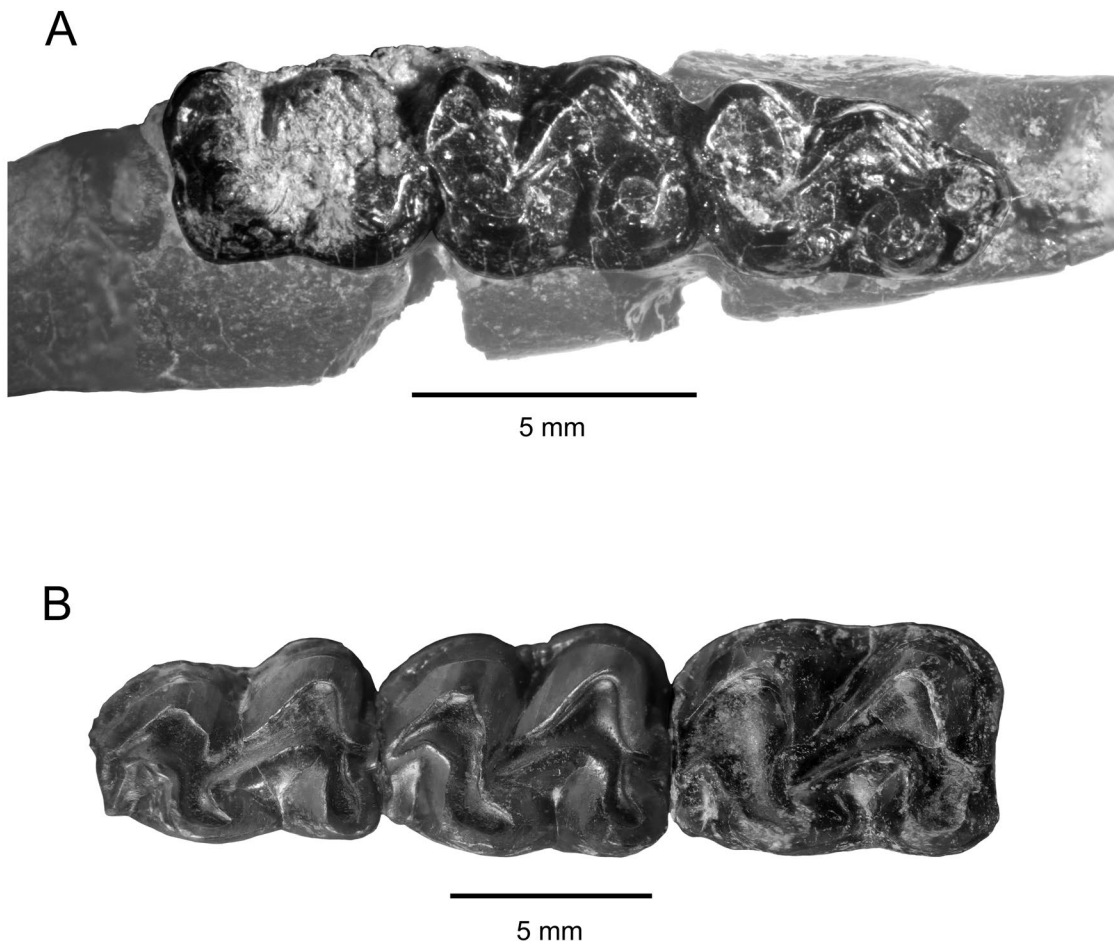


Fig. 17.—**A**, Hyopsodontidae. *Hyopsodus* sp. near *H. paulus*, CM 83372, right mandible with m1–3; **B**, Equidae. *Epihippus* sp. cf. *E. gracilis*, CM 83122, Rp3-m1.

1984, *Metanoiamys lacus* Storer, 1987, *Metanoiamys agorus* Chiment and Korth, 1996, *Metanoiamys marinus* Chiment and Korth, 1996, *Metanoiamys korthi* Kelly and Whistler, 1998, and *Metanoiamys paradoxus* Emry and Korth, 2012, and are known from California and Wyoming. This Kishenehn rodent has lower cheek teeth with an ectolophid, which is reported to be weak or absent in *Metanoiamys* (Chiment and Korth 1996). In the Kishenehn eomyid, p4 is short anteroposteriorly, square in outline, and has a small anteroconid as in *Namatomys* Black, 1965, and the yoderimyines.

The oldest known Asian eomyid is the Ergilian (late Eocene) *Symplokeomys* Emry et al., 1997, of Kazakhstan, which has highly derived dental characteristics for an eo-

myid, shown by complexities of the cusps and lophs of its cheek teeth (Emry et al. 1997). Eomyids probably stem from the sciuravids of North America, suggesting a westward migration pattern of origin.

While Walsh (1997) regarded eomyids, as Myodonta, this assignment is not universally accepted (Wahlert 1978; Flynn 2008), nor is it validated here. In most descriptions of Uintan-Duchesnean eomyids a high degree of seemingly individual variation is described, making accurate comparisons difficult. For example, an anteroconid may or may not be present on p4. Confounding individual teeth of *Metanoiamys*, *Pauromys*, and *Microparamys* appears to be a recurring problem (Walsh 1997), for which no solution is offered here.

Order Condylarthra Cope, 1881
Family Hyopsodontidae Trouessart, 1879

Hyopsodus sp. near *Hyopsodus paulus* Leidy, 1870
Fig. 17A

Referred specimens.—CM 83351, L mandible with partial m3: locality M-2; CM 83352, Lp3-M1; CM 83353, Lm1 or m2; CM 83354, Lm3; CM 83355, Lp4; CM 83356, Lp4; CM 83357, Rp4; CM 83358, Rm1 or m2; CM 83359, partial m3; CM 83360, RM2; CM 83361, LM2; CM 83362, fragmentary RM1 or M2; CM 83363, LM1; CM 83365, fragmentary L mandible with m2-3; CM 83366, LM3; CM 83367, RM2; CM 83368, Rm2; CM 83369, L maxilla with M2; CM 83370, LM2; CM 83371, RM3; CM 83372, R mandible with m1-3: locality M-28R. More anterior cheek teeth were not assigned numbers.

Sample measurements.—CM 83360, RM2, a–p 4.627 mm, w 6.01 mm; CM 83368, Rm2, a–p 4.080 mm, w 2.755 mm; CM 83372, Rm2, a–p 4.496 mm, w 3.320 mm.

The Kishenehn record of *Hyopsodus* Leidy, 1870, both isolated teeth and a few incomplete mandibles with dental remains, does little to reveal its specific determination. Flynn (1991:2, 14) demonstrated for *Hyopsodus* that “defining species and determining their phylogenetic interrelationships has proved particularly problematic” and that “very few uniquely derived features diagnose and distinguish *Hyopsodus* from other early Cenozoic ‘ungulates’ or ‘condylarths’.” Size is considered one of the diagnostic species characters of the genus by Gazin (1968) and West (1979). Some variation in size occurs within the Kishenehn sample but there do not appear to be two species and the currently available material, although abundant by Kishenehn standards, does not warrant a more precise taxonomic allocation. Small size and usual absence of a lower molar metastylid suggest affinities with *H. paulus*, which is known also from the middle and early late Eocene of Wyoming, Utah, Colorado, and Texas (West 1979; Flynn 1991).

In the Eocene of the Holarctic, hyopsodontids were moderately wide ranging and long lasting, occurring from the Wasatchian through the late Duchesnean in North America (Gazin 1968; Redline 1997), the early and middle Eocene of Asia (Dashzeveg 1977; Tong and Wang 2006), and the early Eocene of Europe (Godinot 1978; Hooker 1979). In North America, *Hyopsodus* ranges north to south from Saskatchewan to Texas, but has not been recorded in the later Eocene of California (Walsh 1996b). The Kishenehn *Hyopsodus* is smaller than *H. fastigatus* Russell and Wickenden, 1933, which is recorded from Swift Current Creek (Storer 1984). The genus appears to have been restricted in distribution or ecology late in its temporal range, being absent from the Duchesnean localities Badwater 20 and Lac Pelletier, Saskatchewan, although present in the Duchesnean Shoddy Springs locality of Montana (Krishtalka 1979; Storer 1996). In Asia, *H. orientalis*

Dashzeveg, 1977, was present during the time of the Bumban member (early Eocene) (Dashzeveg 1977), and Tong (1989) has named two Asian species of middle Eocene *Hyopsodus*, one from the Junggar Basin and one from the Turpan Basin. The genus is not known from southern Asia or in the Eocene of the Arctic (Dawson 1990).

Order Creodonta

Referred specimen.—CM 83149 (Half of a lower molar of a probable creodont is the only trace of this taxon in the fauna): locality M-28R.

Order Carnivora Bowdich, 1821
Family Miacidae Cope, 1880

Miacis near *Miacis gracilis* Clark, 1939

Referred specimen.—CM 83148, Rm1: locality M-2.

Sample measurements.—CM 83148, Rm1, a–p 8.119 mm, w 4.170 mm.

The Kishenehn miacid is smaller than the type of *Miacis gracilis* (CM 11900) but larger than *Miacis* species indeterminate (CM 71199) from the early Uintan of Utah (Friscia and Rasmussen 2010). CM 83148 and two fragments of lower teeth (CM 83150, CM 83151) are the only currently known Carnivora in the Kishenehn deposits. CM 83148 is a right lower trigonid, possibly Carnivora, from locality M2. This record does little except emphasize a presumed scarcity of carnivorans living in the area represented in the fauna. It contrasts weakly with the four taxa of Carnivora reported from the Uintan Swift Current Creek, and the five carnivoran taxa from the Uintan and Duchesnean Badwater localities. The carnivoran record from the Uintan of Texas is also sparse, with only the creodont *Sinopa* Leidy, 1871, a miacid indet., and *Miocyon* sp. from Whistler Squat (Campisano et al. 2014). *Miacis* occurs across the Holarctic in the Eocene.

Order Perissodactyla Owen, 1848

The diversity of perissodactyls in the Kishenehn Eocene deposits, five genera within four families, contrasts with the scarcity of artiodactyls, of which there is only one genus. Relative rarity of artiodactyls in the late Eocene of Asia has been linked to an abundance of tapiroids there (Radinsky 1965). Nonetheless, Kishenehn perissodactyls are slightly less diverse in comparison, for example, with those in Uintan deposits at Badwater, Wyoming, where seven genera occur among six families (Black 1979), although more diverse than at Swift Current Creek, Saskatchewan, with four perissodactyl genera among three families (Storer 1984).

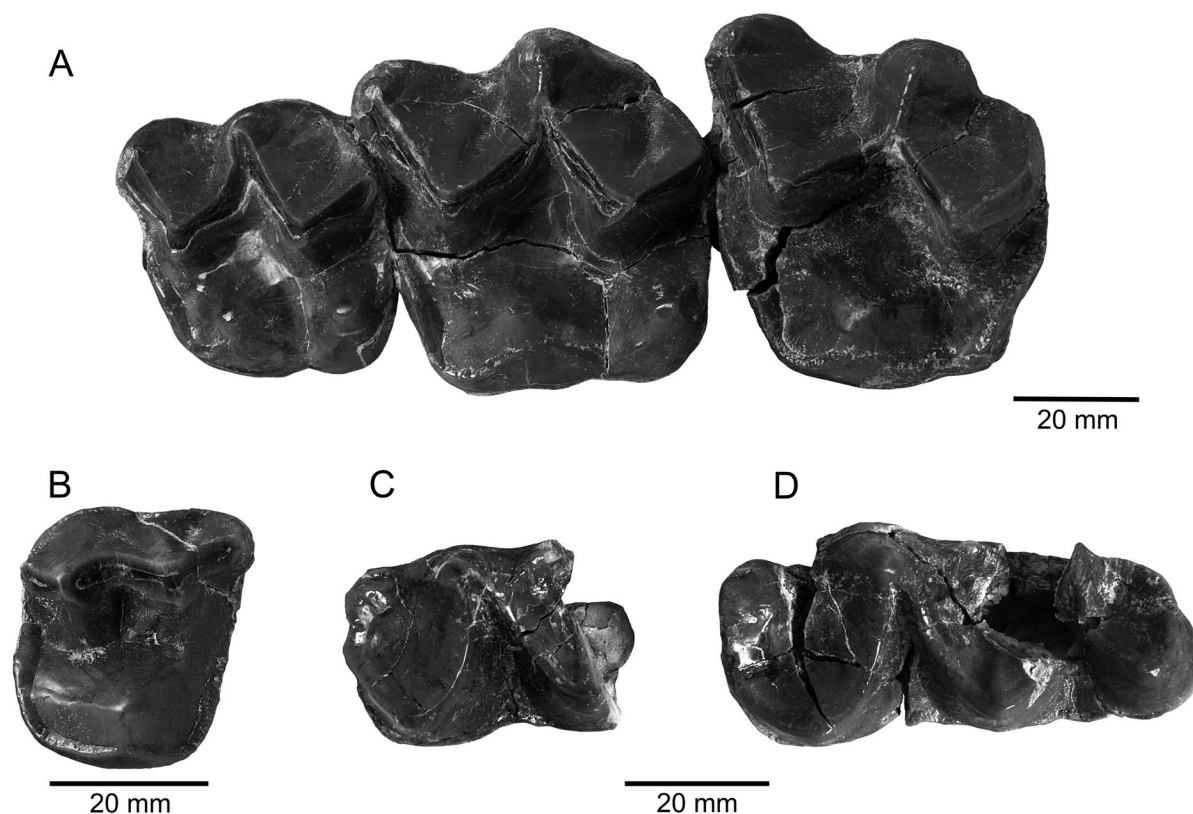


Fig. 18.—Brontotheriid sp. cf. *Dolichorhinus hyognathus*, CM 83140. **A**, LM1-3; **B**, RP4; **C**, incomplete Lm1; **D**, Lm3.

Suborder Hippomorpha Wood, 1937
Family Equidae Gray, 1821

Epihippus sp. cf. *Epihippus gracilis* Marsh, 1878
Fig. 17B

Referred specimens.—CM 83122, Rp3–m1: locality M-2.

Sample measurements.—CM 83122, p3, a–p 6.5 mm, w 4.8 mm; p4, a–p 6.8 mm, w 5.4 mm; m1, a–p 7.9 mm, w 5.5 mm.

The teeth are near the size of Wagonhound *E. gracilis*. Other than in size, the primary differences between species of *Epihippus* are in molarization of the premolars. Because not all premolars are represented in the Kishenehn equid sample, identification of the species represented may be misleading. At Swift Current Creek, the sole equid is *Epihippus* cf. *E. gracilis*, which is relatively poorly represented (six teeth, Storer 1984). Gazin (1956) and Black (1979) included *E. gracilis* and *E. parvus* Granger, 1908, in the Badwater Uintan, the former less abundant. Equids

are absent in the Californian early Uintan, and present but incompletely represented in the Uintan Devils Graveyard of Texas (Campisano et al. 2014).

Suborder Ceratomorpha Wood, 1937

Family Brontotheriidae Marsh, 1873

A recent analysis of brontotheriids (Mihlbachler 2008) postulated recognition of 36 genera of these perissodactyls, all but six of them monospecific, across the Holarctic and ranging in age from the Wasatchian to Chadronian NALMAs. Another analysis, also dating to 2008 but limited to Bridgerian and Uintan brontotheres (Mader 2008), postulated different taxonomic assignments, adding to the difficulty in assigning the two Kishenehn brontotheres to taxa within this assemblage. Many of the characters used to determine affinities, especially those of the skull, horns, and anterior dentition, are currently not known for these Kishenehn herbivores, which are represented mostly by remains of isolated, and sometimes broken teeth. Muhl-



Fig. 19.—Brontotheriid sp., large species, CM 83136. **A**, RM1-3; **B**, left C.

bachler (2008) supported the concept of a North American origin for brontotheres, and recognized nine to 12 intercontinental dispersal events between Asia and North America, their main areas of occurrence, in the middle Eocene (Uintan, Irдинmanhan); of these the direction of immigration for nine was considered to be from North America to Asia, and three, the reverse. Brontotheres are very rare in Europe (Hungary, Bulgaria) with two genera, *Brachydiastematherium* Bockh and Maty, 1876, and *Menodus* Pomel, 1848, presumably in the Eocene (Lucas and Schoch 1989). An indeterminate brontotheriid is represented sparsely in the Uintan Swift Current Creek fauna (Storer 1984), as is a brontotheriid in the Badwater, Wyoming, Duchesnean locality 20, referred to *Telmatherium* cf. *Telmatherium cultridens* Osborn et al, 1878, by Black (1979:393), although “In the absence of diagnostic skull material it is difficult to arrive at a reliable generic determination of this form”; the latter was synonymized with *Telmatherium validus* Marsh, 1872, in Muhlbachler (2008). Upper molars of both Kishenehn brontotheres have small paraconules, a primitive character, which are lacking in many brontotheres (Muhlbachler 2008).

Brontotheriid sp. near *Dolichorhinus hyognathus*

Osborn, 1889

Fig. 18

Referred specimen.—CM 83140, LP2-3, LM1-3, RP4-M1, Lp4-m3, Rm2-3; locality M-3.

In the absence of skull material, identification is problematic, but dental morphology and size appear to place this brontothere close to *D. hyognathus*, which is known to occur in the Wagonhound member of the Uinta Basin, Utah, and the Adobe Town member of the Washakie Basin, Wyoming.

Left P2 (a-p 24.9 mm, w 22.0 mm) is two rooted, with the anterior root smaller. The crown is elongated antero-buccally by a distinct parastyle, a cingulum extends from the parastyle around the tooth to the metacone, but there are only small traces of cingulum on the buccal side. Paracone and metacone are well developed and separate. Lingually oriented crests extend in parallel from the paracone and metacone. There is no trace of a hypocone.

Left P3 (a-p 27.9 mm, w broken) is similar to P2, also having two roots, with the anterior smaller; the paracone

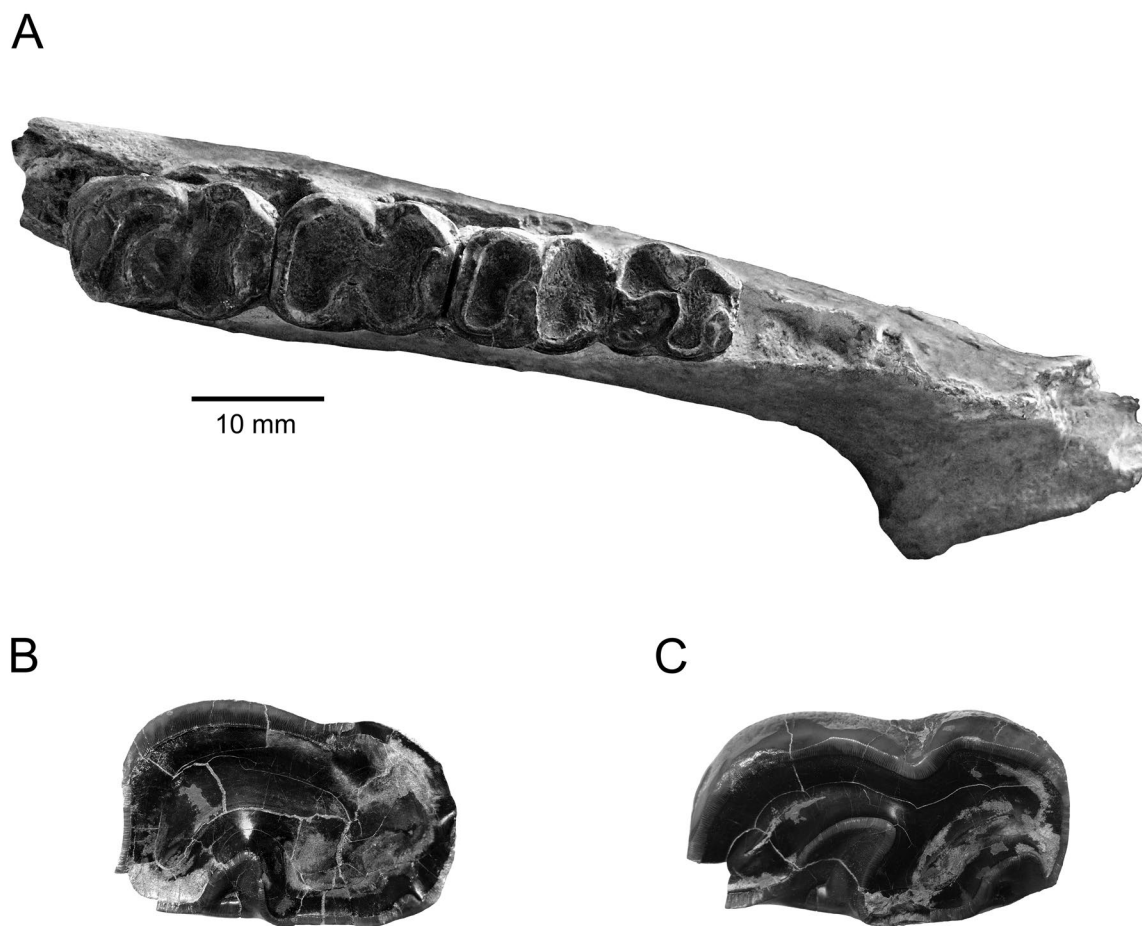


Fig. 20.—Rhinocerotidae. **A**, *Helalestes* cf. *Helalestes intermedius*, CM 83147, occlusal view of left mandible with p4-m3; **B-C**, *Amynodon* sp. near *A. advenus*, CM 83199: **B**, Lm3; **C**, Lm2.

and metacone are subequal, having crests that converge slightly. The hypocone area is broken away.

Right P4 (a-p 29.8 mm, w 36.3 mm) has a paracone with a suggestion of a lingual crest that is oriented toward the protocone. The tooth is broken lingually so there is no evidence of the shape of the protocone or of the morphology of a hypocone.

M1 (a-p 41.5 mm, w 42.2 mm) has a W-shaped ectoloph; the cusps are inclined lingually; there is a small paraconule and a robust hypocone.

M2 (a-p 61.6 mm, w 62.8 mm) resembles M1 but is larger and has a more prominent mesostyle that extends farther buccally. The paraconule is small but distinct.

M3 (a-p 46.8 mm, w 64.2 mm) has a very small paraconule. The tooth is widest at the parastyle; a small hypocone is present.

Although there are broken segments of the mandible, the lower teeth are not preserved as well as the uppers nor do they present diagnostic characters. The longest tooth is

m3 with a length of 66.5 mm and width at the metaconid of 30.7 mm. A narrow anterior cingulid extends from the buccal side of the protoconid to the lingual side of paraconid.

Brontotheriid sp., large species Fig. 19

Referred specimen.—CM 83136, R canine and RM1-3: locality M-40T.

This very large brontothere (Rt M3 a-p 75.5 mm, w 68.5 mm) preserves the upper molar series. The anterior cingulum is narrow, small paraconule and metaconule are present, the protocone is situated near the anteroposterior midpoint of the lingual side, and the hypocone is absent. Several of these characters, including presence of a paraconule, are relatively primitive brontothere characters (Gunnell and Yarbrough 2000); loss of upper molar conules is Muhlbachler's character 66 (2008), although these structures are present in both Kishenehn brontotheres.

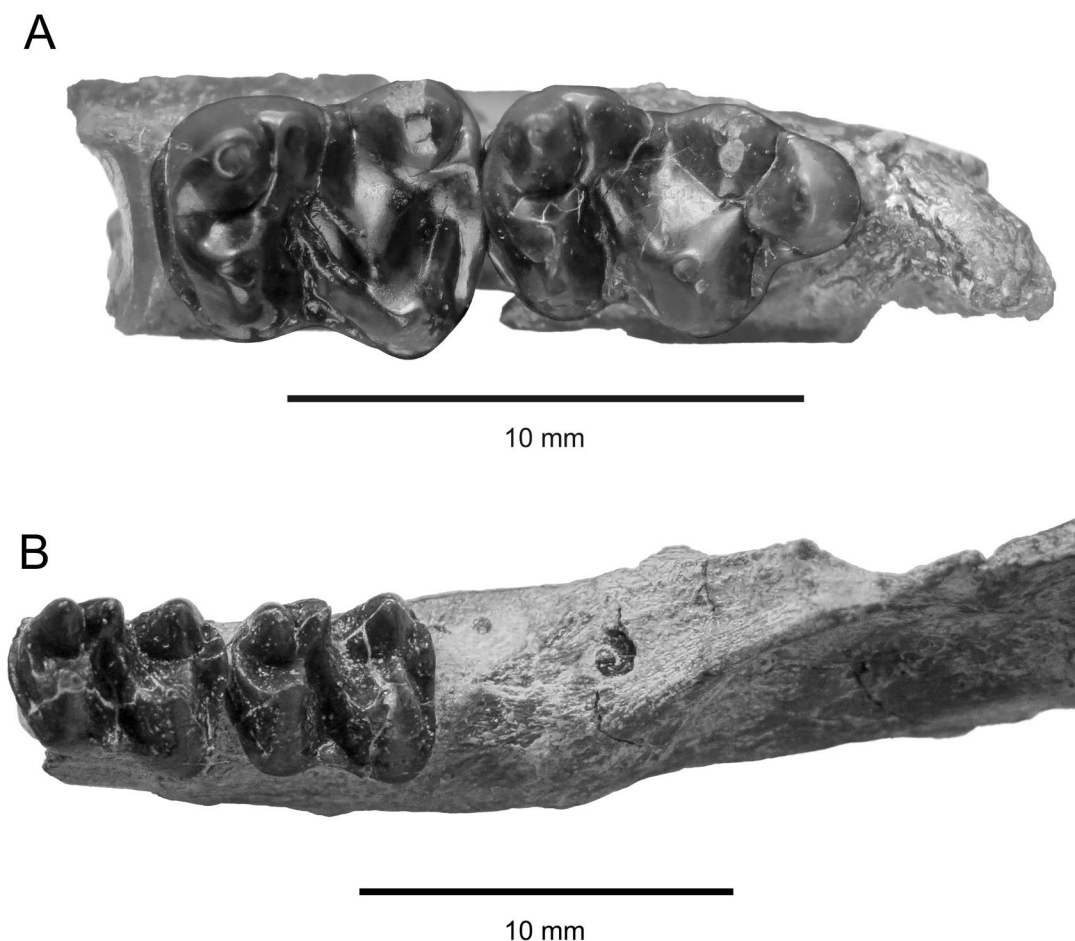


Fig 21—*Antiacodon* sp. cf. *Antiacodon venustus*. **A**, CM 83120, left mandible with m2-3; **B**, CM 83121, left mandible with m1-2.

Superfamily Tapiroidea Burnett, 1830
Family Helaletidae Osborn, 1892

Helaletes cf. *Helaletes intermedius* (Osborn et al., 1878)
Fig. 20A

Specimens.—CM 83147, L mandible with worn p4–m3, other tooth fragments; CM 83141, Rp: locality M-7.

Sample measurements.—CM 83147, p4, a–p 9.5 mm, w 9.2 mm; m1, a–p 12.1 mm, w 9.2 mm; m2, a–p 14.1 mm, w 11.1 mm; m3, a–p 16.6 mm, w 11.1 mm.

As far as can be determined from lower jaw and incomplete tooth morphology, the Kishenehn tapiroid is one of the bilophodont helaletids, which are a relatively closely knit but somewhat poorly differentiated group (Radinsky 1969). In CM 83147, traces of the incisor alveoli are present but due to breakage presence or absence of alveoli for

the lower canine or p1 cannot be determined. The two anterior lower teeth, p2–3, are missing from the specimen while the alveoli show that each was two rooted. The anteriormost teeth preserved, p4–m1, are well worn but m2–3 retain remnants of occlusal morphology. The p4 talonid is slightly wider than the trigonid of m1. The hypoconulid of m3 is small and transversely elongate.

Close similarities appear to be with the North American Bridgerian *Helaletes intermedius* (Osborn et al., 1878) and Asian *Helaletes mongoliensis* (= *Desmatotherium mongoliensis* Osborn, 1923, = *Helaletes mongoliensis* in Radinsky 1965, = *Irdinolophus* in Dashzeveg and Hooker 1997) from the Irdin Manha beds of Inner Mongolia.

The presumably allied tapiroid *Colodon* Marsh, 1890, is first recognized in North America in the later Uintan (Ui3, Gunnell et al. 2009). Individual teeth and tooth fragments of *Colodon* cf. *C. kayi* Hough, 1955, are reported

from Swift Current Creek (Storer 1984) and of *C. woodi* Gazin, 1956, from Badwater localities 5, 6, 7, and Rodent (Black 1979). In their perceptive analysis of *Colodon* cf. *C. hancocki* (Radinsky, 1963) from the late Uintan Candelaria local fauna of Texas, Wilson and Schiebout (1984:11) observed that “the late Eocene tapiroids are poorly known and this material from Texas only extends the geographic range of the taxonomic confusion.” The Kishenehn record does little to alter that conclusion for *Heleletes intermedius*, which has a recent reference to *Desmatotherium intermedius* (Colbert and Schoch 1998).

Superfamily Rhinocerotidea Owen, 1825
Family Rhinocerotidae Gray, 1821
Subfamily Amynodontinae Scott and Osborn, 1883
Amynodon Marsh, 1877

Amynodon sp. near *Amynodon advenus* (Marsh, 1875)
Fig. 20B

Referred specimens.—CM 83199, lower jaw fragments, worn Lm1-3, Rm3, broken lower canine: locality M-5; CM 83198, RP2: locality M-2.

Sample measurements.—CM 83199, Lm1, a-p 14.7 mm, w tr 16.6 mm, w tal 17.2 mm; Lm2, a-p 31.4 mm, w tri 19.4 mm, w tal 20.2 mm; Lm3, a-p 33.9 mm, w tri 18.7 mm, w tal 17.2 mm; CM 83198, RP2, a-p 16.5 mm, w 18.2 mm.

Amynodontids were important Eocene immigrants into North America from Asia that persisted in the former until the early Oligocene. In Asia, they were taxonomically diverse (Dashzeweg and Hooker 1997; Wall 1998), with the Irdiv Manhan (middle Eocene) *Sharamynodon* Kretzoi, 1942, of Inner Mongolia (Lucas and Emry 2001) being the oldest well-defined member of the family. One lineage of amynodonts migrated into Europe in the Oligocene (McKenna and Bell 1997). In North America, amynodontids have been utilized as indicators of earliest Uintan time, with the beginning of the Uintan NALMA defined by the stratigraphically lowest known occurrence of *Amynodon* (Walsh 1996b, although Gunnell et al. (2009) listed the first appearance of *Amynodon* in Ui1b).

In the North American Eocene, *Amynodon* is widely distributed, occurring in the Rocky Mountain region with *Amynodon* sp. present in the Badwater Uintan (Black 1979), *A. advenus* reported by Wood et al. (1936) in “locality 3 but not common,” and in the Shoshonean Subage of the East Fork Basin, Tepee Trail Formation in Wyoming (Flynn 1986). Other occurrences include *A. advenus* in the Uintan of the Uinta Basin, Utah, and the early Uintan Whistler Squat Quarry in southern Texas (Wilson and Schiebout 1981); the small species *A. reedi* Stock, 1939, occurs in California (Stock 1938). *Amynodontopsis* Stock, 1933, is a larger animal that occurs in the Uintan-Duchesnean of California, Texas, South Dakota, and the Rocky Mountain area (Wall 1998). The Kishenehn *Amynodon* is

currently its most northerly record in North America, as the genus is not reported from Swift Current Creek or other localities in Saskatchewan (Storer 1996), absences that may be interpreted to have environmental implications.

Little can be determined for the Kishenehn *Amynodon* due to fragmentary preservation of the known specimens. While it is in the size range of *A. advenus*, its incompleteness precludes definite reference to that species. Presumably, as in other North American localities, it was a cursorial forest-savanna dweller (Wall 1998).

Order Artiodactyla Owen, 1848
Family Homacodontidae Marsh, 1874

Subfamily Antiacodontinae Gazin, 1958

The scarcity of artiodactyls in the Middle Fork deposits, one bunodont taxon, is a striking feature of the Kishenehn assemblage. The early part of the Uintan (especially Ui1b of Gunnell et al. 2009) has been recognized as a time when selenodont artiodactyls such as leptocherids, agriocherids, oromerycids, hypertragulids, and camelids were flourishing elsewhere in North America (Black 1978; Janis 2007). That the only Kishenehn artiodactyl is a relatively primitive one suggests a significantly different situation here from Wyoming faunas, where the selenodont artiodactyls *Leptoreodon* Wortman, 1898, *Protoreodon* Scott and Osborn, 1887, and *Protylopus* Wortman, 1898, have been reported from the Shoshonean (Flynn 1986); at least ten artiodactyl species having a hypocone on P4 were reported from the middle Uintan Badwater faunas, localities 5, 6, 7 (Black 1978), and six species in the Uintan of Swift Current Creek of Saskatchewan (Storer 1984). The Kishenehn record may document a temporal event, possibly reflecting relatively recent immigration of non-North American taxa, or environmental constraints to a more closely forested ecology for the localities rather than a more mixed woodland-type of vegetation (Webb 1977).

A number of selenodont artiodactyls occur in the Uintan and Duchesnean of California (Golz 1976) as well as several taxa of bunodont forms, including *Antiacodon venustus* Marsh, 1872, in the early Uintan Friars Formation of San Diego County, California (Walsh 2000). *Antiacodon* Marsh, 1872, is the only artiodactyl reported from the early Bridgerian Elderberry Canyon fauna of Nevada (Emry 1990).

Antiacodon sp. cf. *Antiacodon venustus* Marsh, 1872
Fig. 21

Referred specimens.—CM 83120, fragmentary L mandible with worn m2-3: locality M-2; CM 83121, fragmentary L mandible with m1-2, unerupted m3: locality Coal Creek.

Sample measurements.—CM 83120, Lm2, a-p 6.051 mm, w 4.618 mm; Lm3, a-p 7.221 mm, w 4.540 mm; CM

83121, Lm1, a–p 5.881 mm, w 4.3 mm; Lm2, a–p 5.671 mm, w 4.876 mm.

This artiodactyl is notably bunodont. As in Bridgerian *Antiacodon*, the lower molar paraconid is larger than the metaconid. The hypoconulid on m1–2 is relatively small and narrow but large and bulbous on m3 (Stucky 1998; Walsh 2000). Known jaws are broken anterior to and below the molars so that any characters of the anterior dentition and shape of the mandible are unavailable and most of the characters differentiating *Auxontodon* Gazin, 1958a, from the closely related *Antiacodon* cannot be established. Lower molar morphology in *Antiacodon* and *Auxontodon* is very similar (Theodor et al. 2007). *Antiacodon* has been reported from the Uintan Poway Formation of California (Walsh 1996a) and a larger, closely allied species, *Auxontodon processus* Storer, 1984, was recorded from Swift Current Creek (Storer 1984). The presence of only one Kishenehn artiodactyl contrasts with the record from Badwater (two bunodont, six selenodont genera) although slightly less with Swift Current Creek (three bunodont, three selenodont taxa; Storer 1984).

DISCUSSION

The Uintan NALMA is a time interval estimated to span approximately 46.2 to 41.3 Ma (Robinson et al. 2004). A somewhat older estimate places the earliest Shoshonean, or the Bridgerian-Uintan boundary, between 48.5 and 49 Ma (Flynn 1986) during a long magnetic reversed interval, Chron C20R. The Uintan is well represented geographically by fossils from North American localities in southern California, the Uinta Basin of Utah, Sand Wash Basin of Colorado, Washakie, Tepee Trail and Wagonbed formations of Wyoming, lower parts of the Renova Formation of southwestern Montana, Swift Current Creek in southern Saskatchewan, the Vieja area of southwestern Texas, and Guanajuato, Mexico. The interval is also known from sites in Asia and Europe. Deposits of the Kishenehn Formation along the Middle Fork of the Flathead River, at about 48° north latitude in and around Glacier National Park, Montana, here add to the fossil record of the early Uintan NALMA, coming from a geologic position stratigraphically above a radiometric age of ca. 46.2 Ma.

Correlation using geologic evidence, fossils, and the radiometric date led to our preliminary age estimate for the Middle Fork deposits. It would be presumptuous to attempt closer temporal correlation for some of the Middle Fork vertebrates solely on the basis of the identifications proposed here, due to their frequently incomplete morphological record, as well as to cautions from previous investigations related to the Bridgerian-Uintan time interval (see Robinson et al. 2004: 117) “There is significant disagreement among members of the committee revising this chapter on the definition of the Uintan and its subunits;” and Gunnell et al. (2009: 291) “The faunal characterization, timing and stratigraphic correlation of the Bridgerian-

Uintan boundary and the Bridgerian-Uintan transitional interval remains one of the most problematic issues of Eocene biochronology”. An additional complexity is that the time interval “Shoshonean” has been inserted between the Bridgerian and Uintan (Flynn 1986). Nevertheless, an attempt is made here to interpret the Middle Fork record, adding its evidence and fitting it into a previously proposed habitat that is based in part on its non-marine invertebrate fossil record (Pierce and Constenius 2014).

Middle Fork taxa and the reported ranges that are here utilized for correlation (Gunnell et al. 2009) include: *Trogolemur myodes* (Bridgerian), *Uintasorex parvulus* (range through to Uila), *Microparamys sambucus* (Bridgerian), *Hyopsodus paulus* (range through Bridgerian), *Helalestes intermedius* (Bridgerian); *Tarkadectes* (“Shoshonean”), *Stockia poweyensis* Gazin, 1958b (Ui1b; note Robinson et al. 2004, listed it as Ui1), leporid (oldest previously reported in Ui2), *Pauromys lillegraveni* (Ui1b), *Metanoiamys* sp. (Ui1a), *Amyndodon advenus* (Ui1b) (used by Flynn 1986, as base of earliest Uintan or Shoshonian; mentioned by McCarroll et al. 1996, as in middle of Washakie Basin’s Adobe Town member; see also Turnbull 1978; Walsh 1996b; Campisano et al. 2014), *Dolichorhinus* (Ui2), and *Antiacodon venustus* (Bridgerian range through taxon, last appearance in Ui1b). Accordingly, the Kishenehn fauna does little to clarify what must remain a problematic time. Neither first nor last appearances, which may reflect environments rather than time, provide a convincing clarification! Nor do they strongly support addition of another time interval, in this case, Shoshonean.

Evidence from fossil plants and invertebrates found near the Kishenehn vertebrate fossils suggests that the animals lived in a humid tropical environment, in an area that was well watered and forested, and offered considerable variation in elevation. The vertebrates themselves are a mixed lot, among which some absences are not expected, such as selenodont artiodactyls and the relatively hypsodont cylindrodontid rodents. These absences tend to support the interpretation that the Kishenehn habitat was riparian with dense, wet adapted vegetation. Storer (1984) discussed presence of bunodont artiodactyls at the Swift Current Creek locality, where there is an equivalent number of selenodonts. The early Uintan age of the Kishenehn fauna may also suggest that the selenodonts had not yet become widely distributed following their Asian (Webb 1977) or North American (Black 1978) origin.

Paleoenvironmental reconstruction of the North Fork region based on freshwater invertebrate taxa and their corresponding modern analogues suggests a valley containing a chain of lakes interconnected by sluggish streams that experienced occasional flooding with formation of transient ponds on the floodplains (Pierce and Constenius 2001). The lakes varied from permanent to semi-permanent, sandy to muddy bottomed, and were generally locally marshy. The ~1000 m thickness of stacked lacustrine strata in the Coal Creek Member of the Kishenehn Formation in the Middle Fork region suggests a more persistent and perhaps

larger perennial lake system in the stratigraphically lower and/or southern-most Kishenehn basin fill deposits. The presence of alluvial fans and fault proximal coarse-clastic detritus derived from the footwall of the Flathead fault system (locally the Roosevelt fault, Fig. 2) combined with faunal, floral and oxygen isotope evidence (Constenius et al. 1989), suggest that densely wooded mountains paralleled the basin to the northeast and rose 2000 m or more above the basin, much as they do today.

The Kishenehn assemblage contributes little to considerations of faunal provinciality in North America during the early Uintan, related to the presumably pronounced environmental factors affecting it. Other analyses have led to interpretation of the post-Bridgerian as a time of increasing provinciality possibly related to regionalized mountain building (Lillegraven 1979; Gunnell et al. 2009; Campisano et al. 2014). Faunal absences such as those of selenodont artiodactyls, rodents including *Sciuravus* and cylindrodontids, and paucity of leporids could well be environmentally controlled. *Tarkadectes*, a relatively rare taxon that is related to *Tarka* from the Tepee Trail Formation of Wyoming and *Tarkops* from the Irdiv Manha of Inner Mongolia, are also suggestive of environmental conditions not often sampled in the fossil record.

Within the Kishenehn fauna several taxa provide evidence on Eocene intercontinental migrations across the Holarctic. Of the 26 currently recognized taxa of Kishenehn mammals, seven are North American only in distribution (*Herpetotherium*, *Oligoryctes*, *Trogolemur*, *Uintasorex*, *Pauromys*, *Epihippus*, *Antiacodon*). *Ectypodus*, *Peradectes*, and *Microparamys* add Europe to their ranges, and the widely distributed *Hyopsodus*, *Amyrnodon*, and *Miacis* occurred across the Holarctic. Thus, Asia has a definite influence on the composition of the Kishenehn fauna, sharing tarkadectines, the primate *Stockia*, leporids, possibly at least some ischyromyids, and *Helalestes*. Brontotheres appear to have been frequent intercontinental migrants with at least twelve North America-Asia dispersals by the middle Eocene (Mihlbachler 2008). Predominance of perissodactyls over artiodactyls in the Kishenehn fauna lends it a generally Asian aspect (Radinsky 1965, 1969).

Comparisons between the Kishenehn fauna and that from the Swift Current Creek, Saskatchewan, Uintan locality, which occurs at about 50° north latitude, support the younger age of the latter. Interesting similarities to the Kishenehn exist with the Bridgerian Elderberry Canyon fauna of Nevada (Emry and Korth 1989; Emry 1990). These may be environmentally related.

Taxonomic diversity within the Kishenehn Formation Middle Fork localities, with 26 taxa recognized, is lower than in the geologically younger locality of Swift Current Creek, Saskatchewan (late Uintan, with 53 mammalian taxa, Storer 1984) and also lower than the richly fossiliferous middle Eocene of Messel, Germany, which has yielded at least 34 genera and 46 species of mammals. On the other hand, absences from the mammalian fauna indicate that lack of certain taxa may be nearly as telling as pres-

ence. The difficulty here is determining relative effects of geologic age and environment. For example, the absences of cylindrodontids and selenodont artiodactyls may relate to environment, in which plants that require mastication of coarse types of vegetation may act as a limiting factor for mammals having dental adaptations for softer plant food. Cylindrodontids occur through a variety of earlier Eocene habitats which makes this absence incline toward environmental constraints. The artiodactyl record, on the other hand, could be partly related to age, with selenodonts probably newly evolved in North America. This may also apply to the scarcity of lagomorphs, which may have arrived in North America, as immigrants from Asia, not long before the time of Kishenehn deposition.

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LITERATURE CITED

- ASHER, R.J., M.C. MCKENNA, R.J. EMRY, A.R. TABRUM, AND D.G. KRON. 2002. Morphology and relationships of *Apternodus* and other extinct zalambdodont placental mammals. *Bulletin of the American Museum of Natural History*, 273:1–117.
- BEARD, K.C., AND M.R. DAWSON. 2009. Early Wasatchian mammals of the Red Hot local fauna, Uppermost Tuscahoma Formation, Lauderdale County, Mississippi. *Annals of Carnegie Museum*, 78(3):193–243.
- . 2014. Northernmost global record for Multituberculata from the Eocene of Ellesmere Island, Arctic Canada. *Journal of Vertebrate Paleontology*, 34 (6):1476–1480.
- BEARD, K.C., AND B. WANG. 1991. Phylogenetic and biogeographic significance of the tarsiform primate *Asiomomys changbaicus* from the Eocene of Jilin Province, People's Republic of China. *American Journal of Physical Anthropology*, 85:159–166.
- BLACK, C.C. 1978. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 14. The artiodactyls. *Annals of Carnegie Museum*, 47(10):223–259.
- . 1979. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 19. Perissodactyla. *Annals of Carnegie Museum* 48(21):391–401.
- BLACK, C.C., AND M.R. DAWSON. 1966. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 1. History of fieldwork and geological setting. *Annals of Carnegie Museum*,

- 38(13):297–307.
- BOURKE, M.R. 2005. Sedimentological and paleoenvironmental analysis of middle Eocene strata of the southeastern Kishenehn Basin, northwestern Montana. Unpublished Masters Thesis, University of California Los Angeles, Los Angeles.
- BRIGGS, D.E.G. 2013. A mosquito's last supper reminds us not to underestimate the fossil record. *Proceedings of the National Academy of Sciences USA*, 110(46):18353–18354.
- BURKE, J.J. 1934. *Mytonolagus*, a new leporine genus from the Uinta Eocene series in Utah. *Annals of Carnegie Museum*, 23:399–420.
- CAMPISANO, C.J., E.C. KIRK, K.E.B. TOWNSEND, AND A.L. DEINO. 2014. Geochronological and taxonomic revisions of the middle Eocene Whistler Squat Quarry (Devil's Graveyard Formation, Texas) and implications for the early Uintan of Trans-Pecos Texas. *PLoS One*, 9(7):1–25.
- CARROLL, A.R., AND K.M. BOHACS. 1999. Stratigraphic classification of ancient lakes: balancing tectonic and climatic controls. *Geology*, 27:99–102.
- CHIMENT, J.J., AND W.W. KORTH. 1996. A new genus of eomyid rodent (Mammalia) from the Eocene (Uintan-Duchesnean) of southern California. *Journal of Vertebrate Paleontology*, 16:116–124.
- COLBERT, M.W., AND R.M. SCHOCH. 1998. Tapiroidea and other moromorphs. Pp. 569–582, in *Evolution of Tertiary Mammals of North America, Volume 1: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals* (C.M. Janis, K.M. Scott, and L.L. Jacobs, eds.). Cambridge University Press, Cambridge.
- CONSTENIUS, K.N. 1981. Stratigraphy, sedimentation, and tectonic history of the Kishenehn Basin; northwestern Montana. Unpublished MS Thesis, University of Wyoming, Laramie.
- . 1982. Relationship between the Kishenehn Basin and the Flathead listric normal fault system and Lewis thrust salient. Pp. 817–830, in *Geologic Studies of the Cordilleran Thrust Belt* (R. Powers, ed.). Rocky Mountain Association of Geologists.
- . 1988. Structural configuration of the Kishenehn Basin delineated by geophysical methods, northwestern Montana and southeastern British Columbia. *The Mountain Geologist*, 25:13–28.
- . 1996. Late Paleogene extensional collapse of the Cordilleran foreland fold and thrust belt. *Bulletin of the Geological Society of America*, 108:20–39.
- CONSTENIUS, K.N., M.R. DAWSON, H.G. PIERCE, R.C. WALTER, AND M.V.H. WILSON. 1989. Reconnaissance paleontologic study of the Kishenehn Formation, northwestern Montana and southeastern British Columbia. Montana Geological Society, 1989 Field Conference Guidebook:189–203.
- CONSTENIUS, K.N., AND J.R. DYNI. 1983. Lacustrine oil shales and stratigraphy of part of the Kishenehn Basin, northwestern Montana. *Mineral and Energy Resources, Colorado School of Mines*, 26(4):1–16.
- CONSTENIUS, K.N., R.P. ESSER, AND P.W. LAYER. 2003. Extensional collapse of the Charleston-Nebo salient and its relationship to space-time variations in Cordilleran orogenic belt tectonism and continental stratigraphy. Pp. 303–353, in *Cenozoic Systems of the Rocky Mountain Region* (R.G. Reynolds and R.M. Flores, eds.). Rocky Mountain Section, Society of Economic Geologists and Mineralogists.
- CURIALE, J.A., S.W. SPERRY, AND J.T. SENFTLE. 1988. Regional source rock potential of Oligocene Kishenehn Formation, northwestern Montana. *Bulletin of the American Association of Petroleum Geologists*, 72:1437–1449.
- DAHLSTROM, C.D.A. 1970. Structural geology in the eastern margin of the Canadian Rocky Mountains. *Bulletin of Canadian Petroleum Geology*, 18:332–406.
- DASHZEVEG, D. 1977. On the first find of *Hyopsodus* Leidy, 1870 (Mammalia, Condylarthra) in the Mongolian People's Republic. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition*, 4:7–13 (in Russian, English summary).
- DASHZEVEG, D., AND J.J. HOOKER. 1997. New ceratomorph perissodactyls (Mammalia) from the middle and late Eocene of Mongolia: their implications for phylogeny and dating. *Zoological Journal of the Linnean Society*, 120:105–138.
- DAWSON, G.M. 1886. Preliminary report on the physical and geological features of that portion of the Rocky Mountains between latitudes 49° and 51°30'. Geological Survey of Canada, Annual Report, n.s., 1, 1885.
- DAWSON, M.R. 1968. Middle Eocene rodents (Mammalia) from north-eastern Utah. *Annals of Carnegie Museum*, 20:327–370.
- . 1970. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 6. The leporid *Mytonolagus* (Mammalia, Lagomorpha). *Annals of Carnegie Museum*, 41(7):215–230.
- . 1990. Terrestrial vertebrates from the Tertiary of Canada's Arctic Islands. Pp. 91–104, in *Canada's Missing Dimension* (C. R. Harrington, ed.), Vols. I and II. Canadian Museum of Nature, Ottawa.
- . 2001. Early Eocene rodents (Mammalia) from the Eureka Sound Group of Ellesmere Island, Canada. *Canadian Journal of Earth Sciences*, 38:1107–1116.
- DAWSON, M.R., L. KRISHTALKA, AND R.K. STUCKY. 1990. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 9. The oldest known hystricomorphous rodent (Mammalia, Rodentia). *Annals of Carnegie Museum*, 59:135–147.
- DEMAISON, G.J., AND G.T. MOORE. 1980. Anoxic environments and source bed genesis. *Organic Geochemistry*, 2:9–31.
- EATON, J.G. 1985. Paleontology and correlation of the Eocene Tepee Trail and Wiggins formations in the North Fork of the Owl Creek Area, southeastern Absaroka Range, Hot Springs County, Wyoming. *Journal of Vertebrate Paleontology*, 5(4):345–370.
- EBERLE, J.J. 2005. A new "tapir" from Ellesmere Island, Arctic Canada—implications for northern high latitude palaeobiogeography and tapir paleobiology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 227: 311–322.
- EBERLE, J.J., N. RYBCZYNSKI, AND D.R. GREENWOOD. 2014. Early Eocene mammals from the Driftwood Creek beds, Driftwood Canyon Provincial Park, northern British Columbia. *Journal of Vertebrate Paleontology*, 34(4):739–746.
- EMRY, R.J. 1990. Mammals of the Bridgerian (middle Eocene) Elderberry Canyon local fauna of eastern Nevada. *Special Paper, Geological Society of America*, 243:187–210.
- EMRY, R.J., AND W.W. KORTH. 1989. Rodents of the Bridgerian (Middle Eocene) Elderberry Canyon local fauna of eastern Nevada. *Smithsonian Contributions to Paleobiology*, 67:1–14.
- EMRY, R.J., B. WANG, L.A. TJUTKOVA, AND S.G. LUCAS. 1997. A late Eocene eomyid rodent from the Zaysan Basin of Kazakhstan. *Journal of Vertebrate Paleontology*, 17:229–234.
- ESCARGUEL, G. 1999. Les rongeurs de l'Eocene inferieur et moyen d'Europe occidentale. Systematique, phylogenie, biochronologie et paleobiogeographie des niveaux-reperes MP7 a MP 14. *Palaeovertebrata*, 28(2–4):89–351.
- FAN, M., K.N. CONSTENIUS, AND D.L. DETTMAN. 2016. Prolonged high relief in the northern Cordilleran orogenic front during middle and late Eocene extension based on stable isotope paleoaltimetry. *Earth and Planetary Science Letters*, 457: 376–384.
- FLYNN, J.J. 1986. Correlation and geochronology of middle Eocene strata from the western United States. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 55:335–406.
- . 1991. *Hyopsodus* (Mammalia) from the Tepee Trail Formation (Eocene), northwestern Wyoming. *American Museum Novitates*, 3007:1–19.
- FLYNN, J.J. 2008. Eomyidae. Pp. 415–427, in *Evolution of Tertiary Mammals of North America, Volume 2: Small Mammals, Xenarthrans, and Marine Mammals* (C.M. Janis, G.F. Gunnell, and M.D. Uhen, eds.). Cambridge University Press, Cambridge.
- FOX, R.C. 1990. The succession of Paleocene mammals in western Canada. *Geological Society of America, Special Paper*, 243:51–70.
- FRISCIA, A.R., AND D.T. RASMUSSEN. 2010. Middle Eocene Carnivora-morpha of the Uinta Basin, Utah. *Annals of Carnegie Museum*, 79(1):51–63.
- GAZIN, C.L. 1956. The geology and vertebrate paleontology of upper Eocene strata in the northeastern part of the Wind River Basin,

- Wyoming. Part 2. The mammalian fauna of the Badwater area. Smithsonian Miscellaneous Collections, 131(8):1–35.
- . 1958a. A new dichobunid artiodactyl from the Uinta Eocene. *Breviora*, 96:1–6.
- . 1958b. A review of the middle and upper Eocene Primates of North America. Smithsonian Miscellaneous Collections, 136(1):1–112.
- . 1968. A study of the Eocene condylarthran mammal *Hyopsodus*. Smithsonian Miscellaneous Collections, 153(4):1–90.
- GODINOT, M. 1978. Diagnoses de trois nouvelles especes de mammiferes du Sparnacien de Provence. *Compte Rendu Sommaire des Seances de la Societe geologique de France*, 6:286–288.
- GOLZ, D.J. 1976. Eocene Artiodactyla of southern California. Los Angeles County Museum of Natural History Bulletin, 26:1–85.
- GREENWALT, D.E., AND K.N. CONSTENIUS. 2014. The middle Eocene Coal Creek member of the Kishenehn Formation, an emerging insect Konservat-Lagerstätten. Abstract, Geological Society of America, 2014:491.
- GREENWALT, D.E., Y.S. GOREVA, S.M. SILJESTROM, T.R. ROSE, AND R.E. HARBACH. 2013. Hemoglobin-derived porphyrins preserved in a middle Eocene blood-engorged mosquito. *Proceedings of the National Academy of Sciences USA*, 110(46):18496–1800.
- GREENWALT, D.E., T.R. ROSE, AND S. CHATZIMANOLIS. 2016. Preservation of mandibular zinc in a beetle from the Eocene Kishenehn Formation of Montana, USA. *Canadian Journal of Earth Sciences*, 53: 614–621.
- GREENWALT, D.E., T.R. ROSE, S.M. SILJESTRÖM, Y.S. GOREVA, K.C. CONSTENIUS, AND J.G. WINGERATH. 2015. Taphonomy of the fossil insects of the middle Eocene Kishenehn Formation. *Acta Palaeontologica Polonica*, 60(4):931–947.
- GUNNELL, G.F., P.C. MURPHEY, R.K. STUCKY, K.E.B. TOWNSEND, P. ROBINSON, J.P. ZONNEVELD, AND W.S. BARTELS. 2009. Biostratigraphy and biochronology of the latest Wasatchian, Bridgerian, and Uintan North American land mammal “ages.” *In* *Papers on Geology, Vertebrate Paleontology and Biostratigraphy in Honor of Michael O. Woodburne* (L.B. Albright, ed.). Museum of Northern Arizona, Bulletin, 65:279–330.
- GUNNELL, G.F., AND V.L. YARBOROUGH. 2000. Brontotheriidae (Perissodactyla) from the late early and middle Eocene (Bridgerian), Wasatch and Bridger formations, southern Green River Basin, southwestern Wyoming. *Journal of Vertebrate Paleontology*, 20(2):349–368.
- HARTENBERGER, J.-L. 1971. Contribution à l’étude de genres *Gliravus* et *Microparamys* (Rodentia) de l’Eocène d’Europe. *Palaeovertebrata*, 4:97–135.
- HONEY, J.G. 1990. New washakiin primates (Omomyidae) from the Eocene of Wyoming and Colorado, and comments on the evolution of the Washakiin. *Journal of Vertebrate Paleontology*, 10:206–221.
- HOOKE, J.J. 1979. Two new condylarths (Mammalia) from the early Eocene of southern England. *Bulletin of the British Museum of Natural History (Geology)*, 32:43–56.
- HUTCHISON, J.H., AND J.E. STORER. 1998. Turtles from the middle Eocene (Uintan) of Saskatchewan, Canada. *PaleoBios*, 18(2 & 3):36–39.
- JANIS, C.M. 2007. Artiodactyl paleoecology and evolutionary trends. Pp. 292–302, *in* *The Evolution of Artiodactyls* (D.R. Prothero and S.E. Foss, eds.). The Johns Hopkins University Press, Baltimore.
- JANIS, C.M., G.F. GUNNELL, AND M.D. UHEN, EDS. 2008. *Evolution of Tertiary Mammals of North America, Volume 2: Small Mammals, Xenarthrans, and Marine Mammals*. Cambridge University Press, New York, 795 pp.
- JANIS, C.M., K.M. SCOTT, AND L.L. JACOBS (EDS.). 1998. *Evolution of Tertiary Mammals of North America, Volume 1: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*. Cambridge University Press, New York, 691 pp.
- KELLY, T.S. 2010. New records of Rodentia from the Duchesnean (middle Eocene) Simi Valley Landfill local fauna, Sespe Formation, California. *Paludicola*, 8(1):49–73.
- KELLY, T.S. AND D.P. WHISTLER. 1998. A new eomyid rodent from the Sespe Formation of southern California. *Journal of Vertebrate Paleontology*, 18:440–443.
- KORTH, W.W. 1984. Earliest Tertiary evolution and radiation of rodents in North America. *Bulletin of Carnegie Museum of Natural History*, 24:1–71.
- KORTH, W.W., R.J. EMRY, AND M.R. MUSSO. 2015. Systematics, cranial morphology, and taphonomy of the eomyid rodent *Adjidaumo minimus* (Matthew, 1903) from the Chadronian (late Eocene), Flagstaff Rim area, Wyoming. *Journal of Vertebrate Paleontology*, 35(6):e1001854.
- KRISHTALKA, L. 1979. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 18. Revision of late Eocene *Hyopsodus*. *Annals of Carnegie Museum*, 48 (20):377–389.
- KRISHTALKA, L., AND C.C. BLACK. 1975. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 12. Description and review of late Eocene Multituberculata from Wyoming and Montana. *Annals of Carnegie Museum*, 45(15):287–297.
- KRISHTALKA, L., R.J. EMRY, J.E. STORER, AND J.F. SUTTON. 1982. Oligocene multituberculates (Mammalia, Altheria): youngest known record. *Journal of Paleontology*, 56:791–794.
- KRISHTALKA, L., AND T. SETOGUCHI. 1977. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 13. The late Eocene Insectivora and Dermoptera. *Annals of Carnegie Museum*, 46 (7):71–99.
- KRISHTALKA, L., AND R.K. STUCKY. 1983. Paleocene and Eocene marsupials of North America. *Annals of Carnegie Museum*, 52(10):229–268.
- LI, G.-Q., AND M.V.H. WILSON. 1994. An Eocene species of *Hiodon* from Montana, its phylogenetic relationships, and the evolution of the postcranial skeleton in the Hiodontidae (Teleostei). *Journal of Vertebrate Paleontology*, 14(2):153–167.
- LILLEGRAVEN, J.A. 1976. Didelphids and *Uintasorex* (?Primates) from later Eocene sediments of San Diego County, California. *Transactions of the San Diego Society of Natural History*, 18(5):85–112.
- . 1979. A biogeographical problem involving comparisons of later Eocene terrestrial vertebrate faunas of western North America. Pp. 333–347, *in* *Historical Biogeography, Plate Tectonics, and the Changing Environment* (J. Gray and A.J. Boucot, eds.). Oregon University Press, Corvallis.
- . 1980. Primates from later Eocene rocks of southern California. *Journal of Mammalogy*, 61:181–204.
- LINDSAY, E. 1968. Rodents from the Hartman Ranch local fauna, California. *PaleoBios*, 6:1–22.
- LIU, J., AND J. MENG. 2013. Eocene ischyromyids (Rodentia, Mammalia) from the Erlian Basin, Nei Mongol, China. *Vertebrata Palasiatica*, 51(4):289–304.
- LIU, J., M.V.H. WILSON, AND A.M. MURRAY. 2016. A new catostomid fish (Ostariophysi, Cypriniformes) from the Eocene Kishenehn Formation and remarks on the North America species of *Amyzon* Cope, 1872. *Journal of Paleontology*, 90(2):288–304.
- LUCAS, S.G., AND R.J. EMRY. 2001. *Sharamynodon* (Mammalia, Perissodactyla) from the Eocene of the Ily Basin, Kazakhstan and the antiquity of Asian amynodonts. *Proceedings of the Biological Society of Washington*, 114: 517–525.
- LUCAS, S.G., AND R.M. SCHOCH. 1989. European brontotheres. Pp. 485–489, *in* *The Evolution of Perissodactyls* (D.R. Prothero and R.M. Schoch, eds.). Oxford University Press, New York.
- MADER, B.J. 2008. A species level revision of Bridgerian and Uintan brontotheres (Mammalia, Perissodactyla) exclusive of *Palaeosyops*. *Zootaxa*, 1837:1–85.
- MCCARROLL, S.M., J.J. FLYNN, AND W.D. TURNBULL. 1996. Biostratigraphy and magnetostratigraphy of the Bridgerian-Uintan Washakie Formation, Washakie Basin, Wyoming. Pp. 25–39, *in* *The Terrestrial Eocene-Oligocene Transition in North America* (D.R. Prothero and R.J. Emry, eds.). Cambridge University Press, New York.
- MCKENNA, M.C. 1990. Plagiomenids (Mammalia: ?Dermoptera) from the Oligocene of Oregon, Montana, and South Dakota, and middle Eocene of northwestern Wyoming. *In* *Dawn of the Age of Mammals*

- in the Northern Part of the Rocky Mountain Interior, North America (T.M. Bown and K.D. Rose, eds.). Geological Society of America Special Paper, 243:211–234.
- McKENNA, M.C., AND S.K. BELL. 1997. Classification of Mammals Above the Species Level. Columbia University Press, New York, 631 pp.
- McMECHAN, R.D. 1981. Stratigraphy, sedimentology, structure and tectonic implications of the Oligocene Kishenehn Formation, Flathead Valley graben, southeastern British Columbia. Unpublished Ph.D. thesis, Queen's University, Kingston, Ontario.
- McMECHAN, R.D., AND R.A. PRICE. 1980. Reappraisal of a reported unconformity in the Paleogene (Oligocene) Kishenehn Formation: implications for Cenozoic tectonics in the Flathead Valley Graben, southeastern British Columbia. Bulletin of Canadian Petroleum Geology, 28:37–45.
- MIHLBACHLER, M.C. 2008. Species taxonomy, phylogeny, and biogeography of the Brontotheriidae (Mammalia, Perissodactyla). Bulletin of the American Museum of Natural History, 311:1–475.
- MUSTOE, G.E., AND W.L. GANNAWAY. 1995. Palm foliis from northwest Washington. Washington Geology, 23(2): 21–26.
- NI, X., J. MENG, K.C. BEARD, D.I. GEBU, Y. WANG, AND C. LI. 2009. A new tarkadectine primate from the Eocene of Inner Mongolia, China: phylogenetic and biogeographic implications. Proceedings of the Royal Society, B, 277:247–256.
- OSTRANDER, G.E. 1984. The early Oligocene (Chadronian) Raben Ranch local fauna, northwest Nebraska: Multituberculata; with comments on the extinction of the Allothia. Transactions of the Nebraska Academy of Sciences, 12:71–80.
- PIERCE, H.G., AND K.N. CONSTENIUS. 2001. Late Eocene-Oligocene nonmarine mollusks of the northern Kishenehn Basin, Montana and British Columbia. Annals of Carnegie Museum, 70(1):1–112.
- . 2014. Nonmarine mollusks of the Eocene Kishenehn Formation, Middle Fork Flathead River, Montana. Annals of Carnegie Museum, 82(4):305–329.
- RADINSKY, L. 1965. Early Tertiary Tapiroidea of Asia. Bulletin of the American Museum of Natural History, 129(2):183–263.
- . 1969. The early evolution of the Perissodactyla. Evolution, 23(2):308–328.
- REDLINE, A.D. 1997. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 13. Systematics and phylogenetic pattern of early Eocene *Hyopsodus* (Mammalia, Condylarthra). Annals of Carnegie Museum, 66(1):1–81.
- ROBINSON, P. 1968. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 4. Late Eocene Primates from Badwater, Wyoming, with a discussion of material from Utah. Annals of Carnegie Museum, 39(19):307–326.
- ROBINSON, P., C.C. BLACK, AND M.R. DAWSON. 1964. Late Eocene multituberculates and other mammals from Wyoming. Science, 145:809–811.
- ROBINSON, P., G.F. GUNNELL, S.L. WALSH, W.C. CLYDE, J.E. STORER, R.K. STUCKY, D.J. FROELICH, I. FERRUSQUA-VILLAFRANCA, AND M.C. MCKENNA. 2004. Wasatchian through Duchesnean biochronology. Pp. 106–155, in Late Cretaceous and Cenozoic Mammals of North America (M.O. Woodburne, ed.). Columbia University Press, New York.
- ROSE, K.D. 2008. Plagiomenidae and Mixodectidae. Pp. 198–206, in Evolution of Tertiary Mammals of North America: Volume 2: Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, New York.
- RUSSELL, L.S. 1935. A middle Eocene mammal from British Columbia. American Journal of Science, 29:54–55.
- . 1954. Mammalian fauna of the Kishenehn Formation, southeastern British Columbia. Annual Report of the National Museum for 1952–53, Bulletin, 132:92–111.
- SCHOCH, R.M. 1985. Preliminary description of a new late Paleocene land-mammal fauna from South Carolina, U.S.A. Postilla, 196:1–13.
- SCHUMAKER, K.K., AND A.J. KIHM. 2006. Multituberculates from the Medicine Pole Hills local fauna (Chadronian) of Bowman County, North Dakota. Paludicola, 6:9–21.
- SCOTT, C.S. 2006. A new erinaceid (Mammalia, Insectivora) from the late Paleocene of western Canada. Canadian Journal of Earth Sciences, 43:1695–1709.
- SETOGUCHI, T. 1975. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 11. Late Eocene marsupials. Annals of Carnegie Museum, 45:263–275.
- SLOAN, R.E. 1966. Paleontology and geology of the Badwater Creek area, central Wyoming. The Badwater multituberculata. Annals of Carnegie Museum, 38:309–315.
- STORER, J.E. 1984. Mammals of the Swift Current Creek local fauna (Eocene: Uintan), Saskatchewan Museum of Natural History, Natural History Contributions, 7:1–158.
- . 1987. Dental evolution and radiation of Eocene and early Oligocene Eomyidae (Mammalia: Rodentia) of North America, with new material from the Duchesnean of Saskatchewan. Dakoterra, 3:108–117.
- . 1988. The rodents of the Lac Pelletier lower fauna, late Eocene (Duchesnean), of Saskatchewan. Journal of Vertebrate Paleontology, 8(1):84–101.
- . 1990. Primates of the Lac Pelletier lower fauna (Eocene: Duchesnean), Saskatchewan. Canadian Journal of Earth Sciences, 27:520–524.
- . 1993. Multituberculates of the Lac Pelletier lower fauna, late Eocene (Duchesnean), of Saskatchewan. Canadian Journal of Earth Sciences, 30(8):1613–1617.
- . 1995. Small mammals of the Lac Pelletier lower fauna, Duchesnean, of Saskatchewan, Canada: insectivores and insectivore-like groups, a plagiomenid, a microsypid and Chiroptera. Pp. 595–615, in Vertebrate Fossils and the Evolution of Scientific Concepts (W.A.S. Sarjeant, ed.). Gordon and Breach, Amsterdam.
- . 1996. Eocene-Oligocene faunas of the Cypress Hills Formation, Saskatchewan. Pp. 240–61, in The Terrestrial Eocene-Oligocene Transition in North America (D.R. Prothero and R.J. Emry, eds.). Cambridge University Press, New York.
- STUCKY, R.K. 1998. Eocene bunodont and bunoselenodont Artiodactyla. Pp. 358–374, in Evolution of Tertiary Mammals of North America, Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals (C.M. Janis, K.M. Scott, and L.L. Jacobs, eds.). Cambridge University Press, New York.
- SZALAY, F.S. 1969. Uintasoricinae, a new subfamily of early Tertiary mammals (?Primates). American Museum Novitates, 2363:1–36.
- SZALAY, F.S., AND S.G. LUCAS. 1996. The postcranial morphology of Paleocene *Chriacus* and *Mixodectes* and the phylogenetic relationships of archontan mammals. Bulletin of the New Mexico Museum of Natural History, 7:1–47.
- THALER, L. 1966. Les rongeurs fossils du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe. Mémoires du Muséum national d'Histoire naturelle, 17:1–295.
- THEODOR, J.M., J. ERFURT, AND G. MÉTAIS. 2007. The earliest artiodactyls. Pp. 32–58, in The Evolution of Artiodactyls (D.R. Prothero and S.E. Foss, eds.). The Johns Hopkins University Press, Baltimore.
- TONG, Y. 1989. A review of middle and late Eocene mammalian faunas from China. Acta Paleontologica Sinica, 26(3):663–682 (in Chinese, English summary).
- . 1997. Middle Eocene small mammals from Liguangqiao Basin of Henan Province and Yuanqu Basin of Shanxi Province, central China. Palaeontologia Sinica, 18, ser. C, 26:1–256 (in Chinese, English summary).
- TONG, Y., AND J. WANG. 2006. Fossil mammals from the early Eocene Wutu Formation of Shandong Province. Palaeontologia Sinica, 192, C, 28:1–195 (in Chinese, English summary).
- TURNBULL, W.D. 1978. The mammalian faunas of the Washakie Formation, Eocene age, of southern Wyoming. Part 1. Introduction, the geology, history, and setting. Fieldiana, Geology, 33:569–601.
- VAN DER VELDEN, A.J., AND F.A. COOK. 1994. Displacement of the Lewis thrust sheet in southwestern Canada: new evidence from seismic reflection data. Geology, 22:819–822.

- WAHLERT, J.H. 1978. Cranial foramina and relationships of the Eomyoidea (Rodentia, Geomorpha). Skull and upper teeth of *Kansasimys*. American Museum Novitates, 2645:1–16.
- WALL, W.P. 1998. Amynodontidae. Pp. 583–588, in *Evolution of Tertiary Mammals of North America, Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals* (C.M. Janis, K.M. Scott, and L.L. Jacobs, eds.). Cambridge University Press, New York.
- WALSH, S.L. 1996a. Theoretical biochronology, the Bridgerian/Uintan boundary, and the “Shoshonian Subage” of the Uintan. Pp. 52–74, in *The Terrestrial Eocene-Oligocene Transition in North America* (D.R. Prothero and R.J. Emry, eds.). Cambridge University Press, New York.
- . 1996b. Middle Eocene mammal faunas of San Diego County, California. Pp. 75–119, in *The Terrestrial Eocene-Oligocene Transition in North America*. (D.R. Prothero and R.J. Emry, eds.). Cambridge University Press, New York.
- . 1997. New specimens of *Metanoimys*, *Pauromys*, and *Simimys* (Rodentia, Myomorpha) from the Uintan (middle Eocene) of San Diego County, California, and comments on the relationships of selected Paleogene Myomorpha. *Proceedings of the San Diego Society of Natural History*, 32:1–20.
- . 2000. Bunodont artiodactyls (Mammalia) from the Uintan (middle Eocene) of San Diego County, California. *Proceedings of the San Diego Society of Natural History*, 37:1–27.
- WALTON, A.H. 1993. *Pauromys* and other small Sciuravidae (Mammalia, Rodentia) from the middle Eocene of Texas. *Journal of Vertebrate Paleontology*, 13(2):243–261.
- WEBB, S.D. 1977. A history of savanna vertebrates in the New World. Part I: North America. *Annual Review of Ecology and Systematics*, 8:355–380.
- WEIL, A., AND D.W. KRAUSE. 2008. Multituberculata. Pp. 19–38, in *Evolution of Tertiary Mammals of North America, Volume 2: Small Mammals, Xenarthrans, and Marine Mammals* (C.M. Janis, G.F. Gunnell, and M.D. Uhen, eds.). Cambridge University Press, New York.
- WEST, R.M. 1979. Paleontology and geology of the Bridger Formation, southern Green River Basin, southwestern Wyoming. Part 3, Notes on *Hyopsodus*. *Contributions in Biology and Geology, Milwaukee Public Museum*, 25:1–52.
- WILSON, J.A., AND J.A. SCHIEBOUT. 1981. Early Tertiary vertebrate faunas, Trans-Pecos Texas: Amynodontidae. *Texas Memorial Museum, Pearce-Sellards Series*, 33:1–62.
- WILSON, R.W. 1940. Californian paramyid rodents. *Carnegie Institution of Washington Publication, Contributions to Paleontology*, 514:59–83.
- . 1949. On some White River fossil rodents. *Carnegie Institution of Washington Publication, Contributions to Paleontology*, 584:29–50.
- WOOD, A.E. 1962. The early Tertiary rodents of the family Paramyidae. *Transactions of the American Philosophical Society*, 52(1):1–261.
- WOOD, H.E., H. SETON, AND C.J. HARES. 1936. New data on the Eocene of the Wind River Basin, Wyoming. *Proceedings of the Geological Society of America*, 1935: 394.
- WOODBURNE, M.O., ED. 2004. *Late Cretaceous and Cenozoic Mammals of North America*. Columbia University Press, New York, 391 pp.